

SOUTHERN AUSTRALIAN SPECIES OF *CHAMPIA* AND *CHYLOCLADIA* (RHODYMENIALES: RHODOPHYTA)

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Summary

REEDMAN, D. J., & WOMERSLEY, H. B. S. (1976).—Southern Australian species of *Champia* and *Chylocladia* (Rhodymeniales: Rhodophyta). *Trans. R. Soc. S. Aust.* **100**(2), 75-104, 31 May 1976.

Five species of *Champia* are recognised on southern Australian coasts. *C. viridis* C. Ag. (including *C. tasmanica* Harvey, *C. oppositifolia* J. Ag., and *C. verticillata* J. Ag.) resembles the type species [*C. lumbricalis* (L.) Desvaux from South Africa] in having numerous scattered longitudinal filaments passing through the diaphragms of the thallus. *C. insignis* Lucas from Tasmania also has scattered longitudinal filaments. Three other species, *C. affinis* (Hook. & Harv.) J. Ag. (including *C. obsoleta* Harvey), *C. zostericola* Harvey (including var. *arcuata* Hook. & Harv. of *C. affinis*) and *C. parvula* (C. Ag.) Harvey var. *amphibolis* var. nov., have only peripheral longitudinal filaments in the thallus. Australian records of the South African *C. compressa* Harvey probably apply to juvenile *C. tasmanica* or to a probably undescribed species on the N.S.W. coast.

One species of *Chylocladia*, *C. grandis*, is newly described. Other Australian species previously referred to *Chylocladia* belong to *Lomentaria* or are relegated to synonyms.

Introduction

Champia Desvaux is in general a well characterised genus (Kyllin 1956) of the family Champiaceae Kuetzing (1843) (syn. Lomentariaceae Naegeli 1847) of the Rhodymeniales and includes numerous species from most coasts of the world. Some 9 species have been credited to southern Australia, and as with so many Australian genera, taxonomic distinctions are uncertain and in some cases the earliest valid names are not in current use.

Chylocladia Greville has been credited with several Australian species, all of which are synonyms of species of *Champia* or other genera. One new species of *Chylocladia* has, however, been found in South Australian waters.

The type species of *Champia* is *C. lumbricalis* (L.) Desvaux (1808, p. 246), from the Cape of Good Hope, South Africa. Although a well-marked species, *C. lumbricalis* has never been studied in detail, and the generic concepts of structure and reproduction are based largely on the European *C. parvula* (C. Agardh) Harvey which has been investigated most recently by Bliding (1928) who reviews earlier studies.

The thallus construction and reproduction of the type species do, however, appear to conform with those of *C. parvula*, and a brief account of the type species is given below.

Champia is characterised by a multiaxial, hollow but septate and thus segmented, usually much-branched thallus which originates from a ring of apical cells (or a ring plus several central cells). These apical cells each cut off a filament of cells which runs longitudinally through the thallus, and from the peripheral filaments the continuous cortical layer of cells originates close to the apex. If a group of central apical cells is present (as in the type species), then longitudinal filaments also occur in the central region throughout the "hollow" thallus. The characteristic transverse diaphragms in the thallus are derived from the longitudinal filament cells very close to the apex, and originate either from alternate cells or ones 2-3 cells apart. Each longitudinal filament cell cuts off cells laterally in one transverse plane, and these link up and divide further to form the characteristic 1 cell thick diaphragm, the peripheral filaments being adjacent to the cortex or sometimes separated by

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one diaphragm cell. The longitudinal filament cells lying between the diaphragms usually cut off one (-3) gland cells. Outer cortical layers may be formed, and in some species an inner cortex of thizoidal filaments develops.

Most species are much branched, and the branches arise from the regions of the diaphragms by development of a ring of apical cells from cortical cells of the parent branch.

Reproductively *Champia* is fairly distinctive. The procarp consists of a 4-celled carpogonial branch borne on a supporting cell (a cortical cell), together with a 2-celled auxiliary cell branch present before fertilisation. The cystocarps are external and sub-spherical to urceolate, ostiolate, containing a carposporophyte with a basal fusion cell and much branched gonimoblast filaments with terminal carposporangia. The inner cells of the pericarp become stellate and form a network ("tela arachnoidea").

Spermatangia are cut off from mother cells derived from the outer cortical cells, and may cover extensive areas of the branches.

Tetrasporangia develop by enlargement of inner cortical cells, they are tetrahedrally divided and occur scattered over the branches.

Species of *Champia* are moderately common along most of the coast of southern Australia, and are commonly mentioned in ecological accounts. In general, however, they do not characterise any communities, though *C. affinis* may be common in shallow water on rock platforms (Womersley 1948, p. 158).

Chylocladia Greville differs from *Champia* in that the cystocarps do not have an ostiole and the carposporophyte consists of a large, basal fusion cell giving rise directly to carposporangia. The thallus construction of the two genera is similar.

CHAMPRIA Desvaux

The structure and reproduction of the type species, *Champia lumbricalis*

Champia lumbricalis (L.) Desvaux (1808, p. 246) is based on *Ulya lumbricalis* Linnaeus (1771, p. 311) from the Cape of Good Hope. The species is a distinct one, and material from Camps Bay, Cape Town, South Africa (G. Dieckmann, 31.viii.1973) has been studied to check on the generic characteristics.

C. lumbricalis is a robust species forming clumps with numerous axes to 15 cm high, arising from an entangled, stoloniferous base. The axes are 2-4 mm thick, terete and linear, with occasional basally constricted branches

with rounded apices. The diaphragms are regular in position, 1-1½ mm apart and largely obscured below by the thick cortex.

The apices have a central group of 7-8 initials and peripheral ring of about 14 initials, resulting in longitudinal filaments passing through the inner part of each diaphragm as well as 14-20 around the periphery. One complete (rarely 2) and two part longitudinal filament cells occur between the diaphragms, bearing 1-3 gland cells. The cortex close to the apex becomes 3-4 cells thick, with a dense outer cortical layer of antichinally elongate cells. In old axes the cortex increases to about 8 cells thick, and a web of rhizoids also develops as an internal layer to the cortex.

The reproductive organs occur on tufts of short, adventitious, branchlets (5-10 mm long and 1-1½ mm thick) formed on the upper half of the axes. Usually the tufts are dense, with numerous, curved (concave adaxially) fertile branchlets, but in some plants cystocarps are borne on single lateral branchlets.

Cystocarps are borne mainly on the adaxial (concave) side of the curved branchlets, often with 2-4 grouped together; they are ovoid with a small ostiole, 1-2 mm in diameter and high. The carposporophyte arises from a basal fusion cell, with a much-branched gonimoblast bearing terminal carposporangia; subterminal cells probably also mature into carposporangia after loss of the terminal ones. The inner cells of the pericarp become stellate, forming a loose tissue, and the outer wall is comparatively thick. Carpogonial branches and early post-fertilisation stages have not been observed.

Spermatia form a continuous covering all around the branchlets, or sometimes largely on the adaxial sides, with the outer cortical cells cutting off 2-4 elongate spermatangial mother cells which then cut off several ovoid spermatangia.

Tetrasporangia occur densely in the branchlets and are transformed from most of the large inner cortical cells; they are slightly pyriform to ovoid, about 100 µm long, and tetrahedrally divided.

The above description of *C. lumbricalis* agrees well in essential generic details with that of Bliding (1928, p. 5) for *C. parvula*, though the latter is much smaller and slenderer, with a much thinner cortex, and has only peripheral longitudinal filaments. There is thus no reason to doubt the generic concept of *Champia* as recognised by Bliding and by Kylin (1956, p. 346).

Key to southern Australian species of *Champia*

1. Thallus with longitudinal filaments scattered through the diaphragms as well as peripheral filaments; branches usually linear, basally constricted or not, not or slightly constricted at the diaphragms; branching irregular or distichous 2
1. Thallus with peripheral longitudinal filaments only; branches usually tapering to base and apex, usually slightly to moderately constricted at the diaphragms; branching irregular or radial 3
2. Branching irregular, often distant; branches linear, (1-)1-2½ mm broad *C. viridis* (p. 77)
2. Branching subdistichous, fairly regularly pinnate; branches 2-5 mm broad, with a basal slender stalk *C. insignis* (p. 81)
3. Thallus segments obscured; hooked branches absent; usually epilithic; cortical cells cutting off, near branch apices, usually several small outer cortical cells at first around their margins, later becoming almost continuous over the thallus as an outer layer and in older parts cutting off further outer cortical cells; inner primary cortical cells, which thus become obscured, are ovoid, 1½-2 times as long as broad, and 20-30 µm broad *C. affinis* (p. 82)
3. Thallus segments clearly defined throughout most of thallus; usually epiphytic on seagrasses or larger algae; cortical cells each cutting off usually only 1(-2) small cells from their corners, so that the single layer of large cortical cells remains clearly defined throughout most of the thallus; cortical cells usually angular, 2-3(-4) times as long as broad 4
4. Branchlets ½-1 mm, branches 1-2 mm, in diameter; cortex essentially single layered throughout; usually one complete longitudinal filament cell between diaphragms; ultimate branchlets often hooked; usually epiphytic on *Posidonia*, *Amphibolis* or larger algae *C. zostericola* (p. 87)
4. Branchlets 1/3-½ mm, branches ½-1 mm, in diameter; cortex mostly single layered but 2-4 cells thick in oldest axes; usually two complete longitudinal filament cells between diaphragms; ultimate branchlets usually linear, rarely hooked; epiphytic on *Amphibolis* *C. parvula* var. *amphibolis* (p. 91)

Champia viridis C. Agardh 1828: 115. Kuetzing 1849: 862.

Corinaldia viridis (C. Agardh) Trevisan 1848: 108.

Champia tasmanica Harvey 1844a: 407, pl. 19; 1847: 78; 1859: 307. J. Agardh 1852: 370; 1876: 306; 1879: 67, pl. 19, figs 10-12. De Toni 1900a: 79; 1900b: 563. Güler 1952: 95. Hooker & Harvey 1847: 402. King *et al.*, 1971: 122(?). Kuetzing 1849: 862; 1865: 30, pl. 84g. Kylin 1931: 29. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 207, fig. 72. May 1965: 362. Okamura 1904: 88. Reinhold 1897: 53; 1899: 45. Shepherd & Womersley 1970: 134; 1971: 165. Sonder 1846: 177(?); 1853: 682; 1855: 518; 1880: 17. Tate 1882: 18. Tisdall 1898: 506. Wilson 1892: 180. Womersley 1950: 176; 1966: 151.

Champia tasmanica var. *gracilis* Harvey 1863, synop.: 27. Sonder 1880: 17. Tate 1882: 18. *Corinaldia tasmanica* (Harvey) Trevisan 1848: 108.

Champia oppositifolia J. Agardh 1901: 27. De Toni 1924: 309. Kylin 1931: 29, pl. 16, fig. 37. May 1965: 362.

Champia verticillata J. Agardh 1901: 26. De Toni 1924: 309. Kylin 1931: 29, pl. 17, fig. 39. May, 1965: 362.

Champia compressa sensu Harvey 1863, synop.: 27 (at least in part—see below).

FIGS 1, 2A-D, 10

Thallus (Fig. 10) usually with several main axes from a stoloniferous base, forming a dense, spreading tuft commonly 5-15(-20) cm high, moderately or slightly adhering to paper, medium to dark red or red-purple in colour. **Axes** (1-12-3 mm broad, usually with numerous irregular branches in 2-4 orders, often sub-opposite, usually less than 1 cm (sometimes 2-4 cm) apart, in older or grazed plants often verticillately branched. All branches terete to slightly compressed, (3-)1-2½ mm broad, linear to slightly curved, basally constricted and with rounded apices. **Diaphragms** ½-1(-1½) mm apart, regular and usually conspicuous in surface view of thallus. **Cortex** of a single layer of compact cells, polygonal and 25-40 µm across in surface view, with an inner cortex of rhizoidal filaments in older parts of robust plants. **Longitudinal filaments** both peripheral and central, with one complete and two part filament cells between each diaphragm.

Cystocarpus scattered over young branches, globular to urceolate, ostiolate, 1-1 mm in diameter. Apparently very few cystocarpic plants have been collected.

Spermatangia forming a continuous layer over branchlets.

Tetrasporangia scattered in young branches, 60-120 µm in diameter.

Type locality. W. Aust.

Type. Herb. Agardh, LD, 26112.

Distribution. From Rottneest L, W. Aust. around southern Australia and Tasmania to Gabo I, Vic., usually on rough-water coasts or in strong currents, from shaded pools to 28 m deep, with a slender form on *Posidonia* in more sheltered waters.

The type specimen of *C. viridis* C. Agardh consists of 8 small branches on mica, and is identical with the later described *C. tasmanica* Harvey (type from Tasmania, in TCD), under which name most specimens of this taxon have been known.

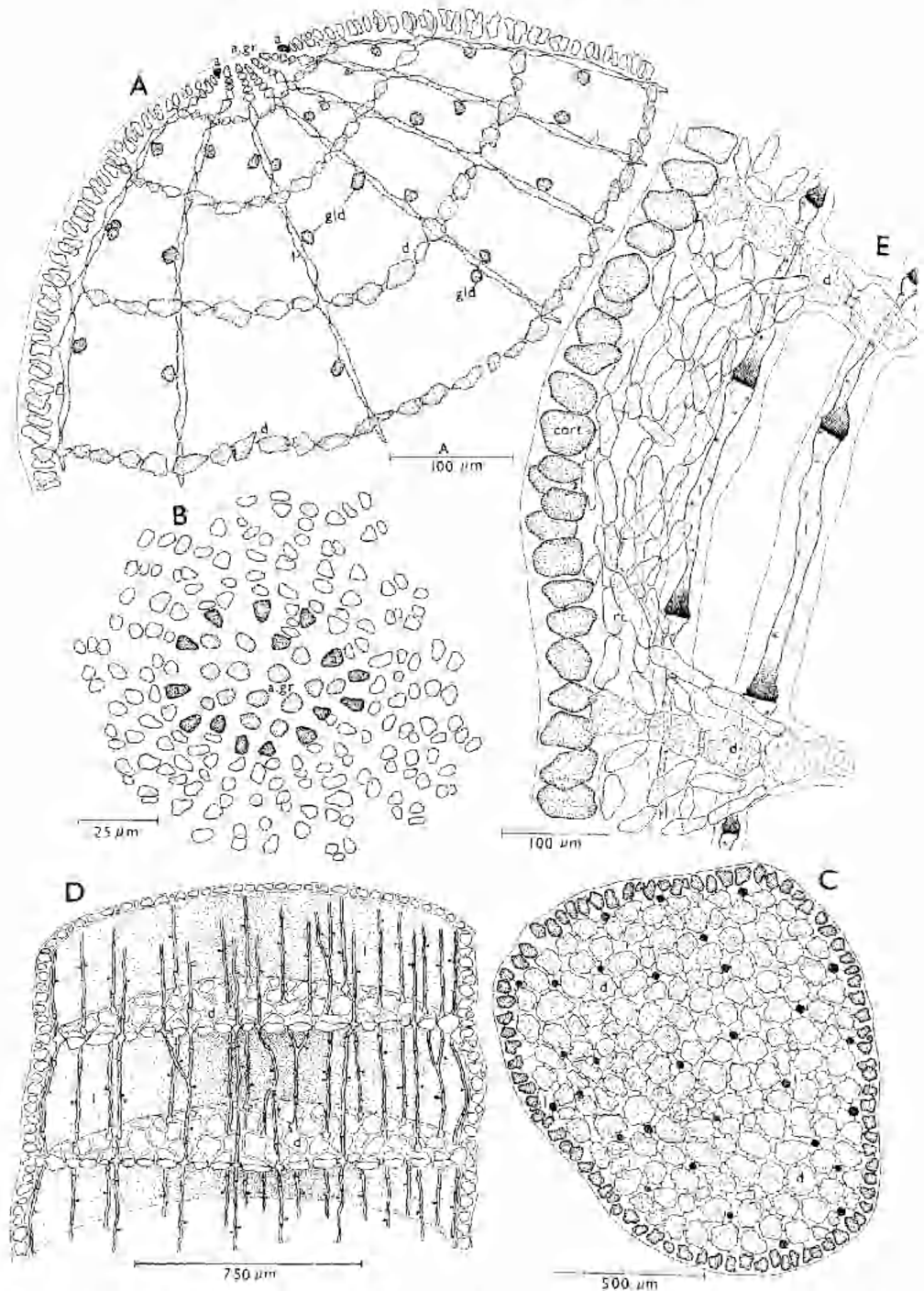


Fig. 1. *Champia viridis*. A. Longitudinal section of a branch apex showing the development of cortex, longitudinal filaments and diaphragms (A42995). B. Surface view of a branch apex showing central and peripheral apical cells (A42991). C. Cross section of a young branch showing a diaphragm with peripheral and scattered longitudinal filaments (A42991). D. Three dimensional view of thallus showing diaphragms and longitudinal filaments with gland cells (A42991). E. Longitudinal section of an older axis showing development of rhizoids from the peripheral diaphragm cells (A30550).

Harvey (1863, *synop.* p. 27) described var. *gracilis* of *C. tasmanica*. A suitable lectotype is probably Harvey's, Alg. Aust. Exsicc. 251, in TCD, from Port Phillip, Vic., and specimens in MEL (45227) from Brighton, Port Phillip, Vic. (Harvey, Trav. Set 483), named var. *fracta*, are probably the same. These are small, slender forms, often found on *Posidonia* under moderate conditions of water movement (e.g. Port Phillip, Vic., St Vincent Gulf, S. Aust.) in early summer, and doubtfully justify a varietal name. The thallus is usually 4–10 cm high, densely tufted with an entangled base, irregularly branched, with occasional curved branch apices, branches mostly $\frac{1}{2}$ –1 mm broad and segments $\frac{1}{2}$ –1 times as long as broad, slightly constricted at the diaphragms. The cell structure is very similar to larger forms typical of the species, with cells about 40 μ m broad, (1–)2–3 times as long as broad, angular with small cells cut off from the corners (about as many small cells as parent cells). While extremes of this sheltered-water form and the robust rough-water form appear relatively distinct, a good range of intergrades does occur.

C. verticillata J. Agardh (1901, p. 26) is based on a specimen (type in LD, 26078) from Port Elliot, S. Aust. (*Hussey*) and is an older plant of *C. viridis* with verticillate branching, and *C. oppositifolia* J. Agardh (1901, p. 27), with type in LD (26148) is a plant with somewhat more distinct opposite branching.

C. viridis is a distinctive species in size, form, and in having central as well as peripheral longitudinal filaments. It varies considerably in robustness and thickness of branches and in branching, with frequent occurrence of proliferous branches giving a subverticillate arrangement. These variations are either ecological or due to the age of the plant.

C. viridis is most closely related to the type species, *C. lumbricalis*, from South Africa, but

is distinct in being a less robust plant and not developing a cortex several cells thick.

A Preiss specimen in MEL (45206) is *C. zostericola*, not *C. viridis*, but a small form of the latter does occur in Western Australia.

C. viridis (as *C. tasmanica*) has been recorded from New Zealand by Naylor (1954, p. 658). This record has not been checked, but may apply to the closely related but distinct *C. novae-zelandiae* Hooker & Harvey, which has central longitudinal filaments but a many layered cortex.

STRUCTURE AND REPRODUCTION

Material studied: Nora Creina, S. Aust., uppermost sublittoral (*Reedman*, 12.ii.1973; ADU, A42995); Cape Lannes, S. Aust., under ledges (*Reedman*, 10.ii.1973; ADU A42991); and Stapleton Point, Prosser Bay, Tas., 8–12 m deep (*Olsen*, 21.vi.1966; ADU, A30550).

Thallus development. The apex of a branch (Fig. 1A, B) includes both a central group of 12–16 initials and a peripheral ring of initials, producing longitudinal filaments passing through the central as well as the peripheral regions of the diaphragms (Fig. 1C, D), as in the type species. The number of central longitudinal filaments is commonly greater than the number of apical initials, due apparently to division of the initials and consequent branching of the filaments and subsequent loss of some initials and termination of some filaments at diaphragms. The apical initials of the peripheral ring divide transversely, and within 2 or 3 cells of the apex divide periclinally forming cortical cells which then divide anticlinally to form the single-layered cortex (Fig. 1A). Alternate cells of the longitudinal filaments cut off cells laterally which join to form the single-layered diaphragms (Fig. 1A), after which the longitudinal filament cells become very elongate. The alternate cells of the longitudinal filaments, lying between the diaphragms, form 1(–2) gland cells (Fig. 1D). Only the cortical cell formed directly from the longitudinal fila-

Abbreviations used in Figures 1–9.

a	— apical cell	fc.b	— fused carpogonial branch	o	— ostiole
a.gr.	— apical group	fu	— fusion cell	per	— pericarp
a.m.c.	— auxiliary mother cell	gl, g2	— gonimoblast cells	r.c.	— rhizoidal cell
aux.	— auxiliary cell	gl	— gonimolobe	sp.	— spermatangium
c.b.	— carpogonial branch	gld	— gland cell	sp.m.	— spermatangial mother cell
co	— outer cortical cell	l	— longitudinal filament	su	— supporting cell
cort	— inner cortical cell	lc	— lateral connecting cell	†	— tela arachnoidea
esp.	— carposporangium			tr	— trichogyne
d	— diaphragm			lspg	— tetrasporangium

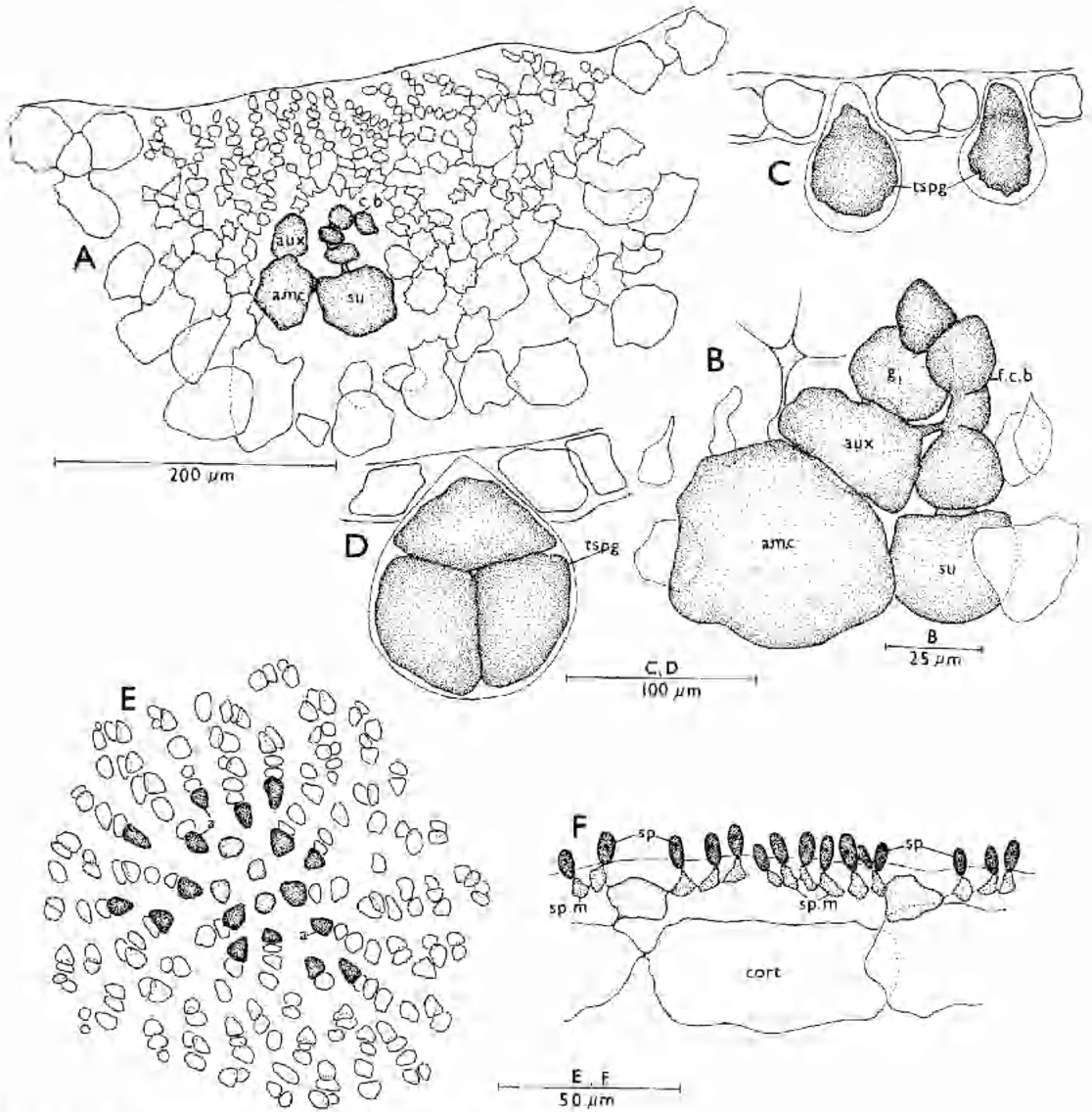


Fig. 2. *Champia viridis*. A. An early post-fertilisation stage showing supporting cell with auxiliary cell branch and carpogonial branch with fusions occurring between the cells. Considerable cortical proliferation has occurred towards formation of the pericarp (A30550). B. A post-fertilisation stage showing a connection between the fused carpogonial branch and the auxiliary cell, and formation of the first gonimoblast initial (A30550). C. Development of tetrasporangial initials (A30550). D. A mature tetrasporangium (A30550). *Champia insignis*. E. Surface view of a branch apex showing initials (A12237). F. Section of male thallus showing development of spermatangia (A12237).

ment cell is in pit-connection with it. In older parts, some cortical cells may produce small outer cells from their corners, but the cortex remains essentially only one cell thick.

In older branches, rhizoidal cells develop from peripheral diaphragm cells and form a loose layer lining the inner side of the cortex (Fig. 1D), as in the type species.

Branches arise from the region of the diaphragms, following development of a group of apical initials from the cortical cells.

Procarp and carposporophyte

Cystocarpic specimens appear to be rare, and only one female specimen with very young carposporophytes has been available. The carpogonial branch is 4-celled and borne on a

supporting cell which also bears the auxiliary mother cell with its auxiliary cell (Fig. 2A). Following fertilisation, the cells of the carpogonial branch fuse and a connection between the fused carpogonial branch and the auxiliary cell is formed (Fig. 2B), and the first gonimoblast cell is cut off from the auxiliary cell. Early post-fertilisation development is accompanied by division of the surrounding cortical cells to form the pericarp (Fig. 2A), and in the one specimen (Stenhouse Bay, S. Aust., 3-7 m deep, Kraft, 18.ix.1973; ADU, A44564) observed with cystocarps, the structure of the pericarp and carposporophyte is typical of *Champia* and very similar to the illustrations of Bliding (1928) for *C. parvula*.

Spermatangia

Spermatangial plants have not been observed.

Tetrasporangia

Tetrasporangia develop by enlargement of cortical cells (Fig. 2C, D) and are tetrahedrally divided, 60-120 μ m in diameter when mature, and scattered in younger branches.

NOTES ON *CHAMPIA COMPRESSA*

Champia compressa Harvey (1838: 402; 1847: 78, pl. 30) was first recorded from Australia by Harvey (1863, synop.: 27) on the basis of specimens from Western Australia (Clifton, and Alg. Aust. Exsicc. 250A) and from Port Fairy, Vic. (Alg. Aust. Exsicc. 250D). Since then, *C. compressa* has been recorded from Australia by the following authors, probably largely on the basis of Harvey's records: Garnet 1971: 96. Lucas 1909: 34. Lucas & Perrin 1947: 206. May 1947: 275; 1965: 362. Sonder 1880: 17(?). Tisdall 1898: 506.

However, comparison with material of *Champia compressa* from St James, Simonstown, S. Africa (G. Dieckmann, 29.iii.1973; ADU, A44601) shows that the Australian records almost certainly are not *C. compressa*. The South African species has strongly compressed branches with numerous central longitudinal filaments scattered across the diaphragms. Harvey's Western Australian specimens also have central longitudinal filaments but the branches are only slightly compressed. They agree in these features with *C. viridis* C. Agardh, and are very similar to young, well displayed, specimens of this species from elsewhere in southern Australia. Harvey's Alg. Aust. Exsicc. 250D (in TCD) from Port Fairy, Vic., includes *C. viridis* as well as some plants

which are not a *Champia*, and one specimen of 250D in BM is *C. zostericola*.

Other records of *C. compressa* from southern Australia probably apply to *C. viridis* if the specimens have central longitudinal filaments, but the records of May (1947, p. 275; 1965, p. 362) from N.S.W. apply to a separate species which may be unnamed. This small, iridescent species, with branches attached to others by haptera, does not have central longitudinal filaments and is only slightly compressed. It is thus distinct from both *C. viridis* and *C. compressa*, and also differs from the very strongly flattened subtropical *C. vieillardii* Kuetzing, which from material from the Solomon Islands (Womersley & Bailey 1970, p. 321) is so strongly flattened that the diaphragms are only 2-4 cells across in the direction of flattening of the thallus, and longitudinal filaments are almost entirely around the periphery.

It is therefore considered that *Champia compressa* does not occur on Australian coasts. Other records of this species from outside South Africa also need checking; the record of Weber van Bosse (1928, p. 477) from Borneo is probably *C. vieillardii*, and that of Joly (1965, p. 176) from Brazil probably applies to a different species.

Champia insignis Lucas 1931: 409, pl. 25, fig. 1. Guiler 1952: 94. Lucas & Perrin 1947: 207. May 1965: 362.

FIGS 2E, F, 11A

Thallus (Fig. 11A) with one to several main axes to 18 cm high, arising from a small, discoid to slightly lobed holdfast on pebbles or shells; branches of pyramidal form, with lower laterals often similarly branched; thallus adhering closely to paper, colour red-brown (herbarium specimens) to "bright purple" (Lucas). Axes 3-5 mm in diameter, subterete (possibly slightly compressed), linear, bearing alternate or opposite laterals mostly $\frac{1}{2}$ -1 cm apart and sub-distichously arranged along the axes, often somewhat denuded towards the base. Main lateral branches usually with a slender stalk (Fig. 11A), then broadening, linear or gently tapering, usually 3-5 mm in diameter, with a rounded apex. Lesser branches similar but slenderer and shorter. *Diaphragms* apparent throughout most of the thallus, 2-3(-4) mm apart in older parts, 1-2 mm apart in younger branches which are slightly constricted at the diaphragms. *Cortex* essentially one cell thick, the cells subpolygonal in surface view, mostly

50–100 μm long and 35–50 μm broad, cutting off 1–3 small cells from their outer corners and more numerous such cells near the thallus base. *Longitudinal filaments* scattered throughout the diaphragms, consisting of several (?) cells between diaphragms.

Cystocarps scattered over the lesser branches, conical to urceolate, ostiolate, 2–11 mm in diameter; carposporophyte branched with lower sterile cells and terminal carposporangia.

Spermatangia cut off from cortical cells (Fig. 2F) and forming collar-like patches on either side of the diaphragms of lesser branches.

Tetrasporangia scattered over the lesser branches, tetrahedrally divided, 80–100 μm in diameter.

Type locality. R. Derwent Estuary, Tas. ("Sandy Bay, Hobart. Oct. 1925" on type sheets.)

Lectotype. Herb. Lucas, NSW, 136559. Syn-types (δ) in NSW (136558) and ADU (A12237).

Distribution. Only known from the type collection and the following Tasmanian collections; D'Entrecasteaux Channel, Nov. 1910 (NSW, 136561); Browns River, Lucas, Oct. 1923 (NSW, 136562); and Snug, Lucas, Aug. 1925 (NSW, 136560). Two specimens in the BM, labelled "Tas. Oldfield", one numbered 81, are probably also from the Derwent Estuary. The species appears to be known only from, or just south of, the Derwent Estuary.

Lucas did not specify type material, but the one now selected as lectotype is the cystocarpic specimen illustrated by Lucas (1931, pl. 25, fig. 1).

The above description is compiled from that of Lucas (1931, p. 409) and study of the type and other material in NSW and ADU. *C. insignis* has apparently not been collected recently, but it seems to be a quite distinct species. It resembles *C. viridis* in having peripheral and central apical cells (Fig. 2E) producing longitudinal filaments scattered across the diaphragms, but differs in form and dimensions and in being essentially distichously branched. Lucas (1931, p. 409) refers to the whole plant as being "compressed". It is desirable, however, that liquid preserved collections should be studied to confirm such aspects.

The BM specimens agree well with the type collection though the lateral branches do not appear to be themselves distichously branched,

and the main branches are basally constricted but scarcely stalked; they are cystocarpic. In carposporophyte structure and the ostiolate cystocarp, *C. insignis* appears to conform well with *Champia*.

Champia affinis (Hooker & Harvey) J. Agardh 1876: 304. De Toni 1900a: 75, pl. 5, fig. 2; 1900b: 559; 1924: 307. Guiler 1952: 94. Harvey 1855a: 545(?); 1859: 307; 1863, synop.: 27. Kylin 1931: 28. Lucas 1909: 34; 1929a: 19; 1929b: 50. Reinbold 1897: 53; 1899: 45. Sonder 1880: 17. Tisdall 1898: 506. Wilson 1892: 180.

Chylocladia affinis Hooker & Harvey 1847: 402. Harvey 1847: 79, pl. 29(?).

Lomentaria affinis (Hooker & Harvey) Kuetzing 1849: 863. J. Agardh 1852: 730. Sonder 1853: 693.

Gastroclonium affine (Hooker & Harvey) Kuetzing 1849: 866.

Chylocladia kaliformis sensu Harvey 1844b: 444.

Champia obsoleta Harvey 1859: 307; 1863, synop.: 27. J. Agardh 1876: 304. De Toni 1900a: 75, pl. 5, fig. 3; 1900b: 559; 1924: 307. Guiler 1952: 94. Kylin 1931: 28, pl. 15, fig. 35. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 206. May 1965: 362. Reinbold 1898: 46. Sonder 1880: 17. Wilson 1898: 506. Womersley 1950: 176; 1966: 150.

FIGS 3, 4, 11B, 12

Thallus (Figs 11B, 12A, B) erect, usually 4–15(–40) cm high, with one to several main axes from a small discoid holdfast, grey-red to purple in colour, adhering to paper; usually growing on rock or on *Amphibolis*, rarely on *Posidonia*. *Axes* usually densely and irregularly radially branched for 3 or 4 orders, branches of pyramidal form (more spreading in plants on seagrasses), often denuded below; axes 1–3½ mm, branches 4–1½ mm, and lesser branches ½–½ mm, in diameter, all branches slightly basally constricted and tapering to rounded apices. *Diaphragms* usually fairly distinct in lesser branches, obscured on older axes, (1–)1–1½(–2) mm apart (segments (½–)1–1½ times as long as broad), thallus constricted at diaphragms except on older axes. *Cortex* of a layer of large sub-ovoid cells, (20–)25–40(–60) μm across, and a sparse layer of outer small cells around margins of inner cells in young branches (Fig. 3F, I), becoming more or less continuous on older parts (Fig. 3G–I) and near bases of old plants 2–4 cells thick (Fig. 3E). *Longitudinal filaments* usually confined to periphery of the diaphragms (Fig. 3C), rarely with 1 or 2 within the periphery, usually with two (occasionally

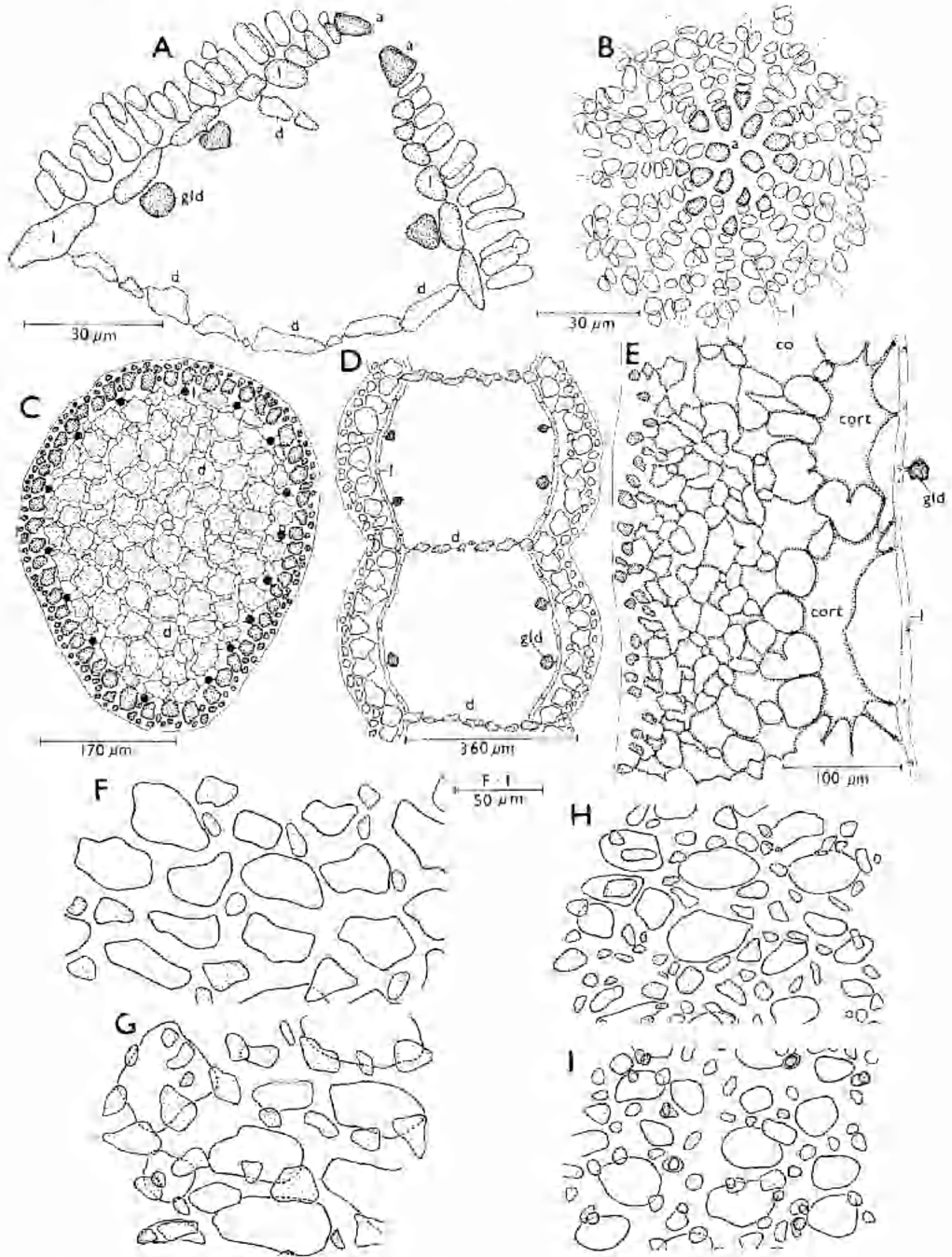


Fig. 3. *Champia affinis*. A. Longitudinal section of a branch apex showing the development of cortex, longitudinal filaments and diaphragms (A42994). B. Surface view of a branch apex showing apical cells (A42994). C. Cross section of a mature branch showing a diaphragm with peripheral longitudinal filaments and small outer cortical cells (A42994). D. Longitudinal section of a mature branch (A42993). E. Longitudinal section of an old axis showing several layers of cortical cells (A42997). F. Surface cell pattern of type specimen (Gunn, in BM) 10 segments from a branch apex. G. Ditto, 30 segments from a branch apex. H. Ditto for Harvey, Alg. Aust. Exsicc. 2521 from Georgetown, Tas., as *C. obsoleta*, 30 cells from a branch apex. I. Ditto for A42990, 10 segments from a branch apex.

one or three) complete cells and two part cells between the diaphragms.

Cystocarps single, scattered over lesser branches, subspherical to urceolate, 1–1½ mm long, ¾–1¼ mm in diameter, with a distinct ostiole (Fig. 4C).

Spermatangia (Fig. 4E) in patches around branchlets on either side of diaphragms, often covering most of the segments.

Tetrasporangia scattered over branches, 60–80 µm in diameter (Fig. 4F).

Lectotype locality. Georgetown, Tas. (Gunn).

Lectotype. BM.

Distribution. From King George Sound, W. Aust. to Western Port, Vic., and around Tasmania. Generally found in shallow water on reefs on rough-water coasts, rarely epiphytic on *Posidonia* or robust algae.

C. affinis was reported from New Zealand by Harvey (1855b, p. 236) and recently by Chapman & Dromgoole (1970, p. 145). There are also specimens in BM from New Zealand, but while they appear closely related to *C. affinis* there are differences in form. Detailed comparisons of liquid-preserved material are needed to establish the relationships of the New Zealand plant.

Hooker & Harvey (1847, p. 402) based *C. affinis* on plants from Georgetown, and a cystocarpic plant in BM has been selected as lectotype (Fig. 11B). Other specimens in BM and in TCD are syntypes. The type specimens are of loose, spreading form and typical of plants from moderately sheltered conditions; the diaphragms are not conspicuous and the wall has an outer layer of small cells which becomes continuous in older parts.

Some of these Georgetown specimens are referred by Harvey to *C. obsoleta*, which he described (1859, p. 307) on the basis of thallus structure and cystocarpic plants, referring to "Alg. Exsic. n. 252" and the following localities:

"HAB. Georgetown. Southport, *C. Stuart*."

DISTRIB. Port Fairy, Victoria. *W.H.H.*"

The critical specimens in TCD include

1. "Georgetown. Sept. 1848. 252 I". This specimen (Fig. 12A) was previously considered the lectotype (by H.B.S.W. in 1952), but is tetrasporangial and has no name on the sheet; it is an old plant but is *C. affinis*, being very similar to the type of this species. Another specimen labelled "Georgetown,

V.D.L. 252 I" is also an old, battered specimen, probably of *C. affinis*.

2. "Southport, V.D.L. *C. Stuart*"—four specimens, two with "*C. obsoleta*" on the sheets, and which are *C. affinis*. They are all tetrasporangial and do not match the type description at all well.
3. "Port Fairy, Vic. *W.H.H.* 252 D"—five specimens, 3 tetrasporangial and 2 cystocarpic; these match the description well and include the only cystocarpic specimens in TCD. One tetrasporangial specimen has "*Champia obsoleta*" on the sheet.

On the basis that the lectotype specimen of *C. obsoleta* should have Harvey's number 252 on it and should also agree well with the type description and be cystocarpic, one of the two Port Fairy specimens (Fig. 12B) is now selected as the lectotype and the other Port Fairy specimens are then syntypes.

In describing *C. obsoleta*, Harvey (1859, p. 307) stated "perhaps only a variety of *C. affinis*", and Kylin (1931, p. 28) doubted that they were distinct species. Study of Harvey's Georgetown material, the Port Fairy specimens of *C. obsoleta*, and knowledge of this common species along southern Australian coasts, suggests strongly that only one species is involved, and *C. obsoleta* is therefore reduced to synonymy. *C. affinis* occurs mainly on rocks and platforms at about low tide level, and under rough-water conditions in such habitats it is of pyramidal form and grey-purple in colour, as Harvey (1859, p. 307) noted. While normally epilithic, it occasionally occurs on other robust algae or on the seagrass *Amphibolis*, and some of Harvey's Georgetown specimens were growing on *Posidonia*. While there appear to be no structural differences between these forms on seagrasses and the rough-water forms, the former are more loosely branched and of more spreading habit.

The type specimen of *C. affinis* shows numerous small outer cells cut off from the primary cortical cells (Fig. 3F, G), but not as many as in rough-water forms (Fig. 3I). However, the habit, lack of clearly visible primary cortical cells and obscuring of the diaphragms in most of the thallus, are features of *C. affinis* as understood here, and differentiate this species from *C. zostericola* (see below). The type of *C. affinis* and other specimens (e.g. in ADU) from Georgetown in Tasmania, Port Phillip Heads in Victoria, and near American River inlet on Kangaroo Island, appear to represent relatively calm water forms of the species.

and the type of *C. obsoleta* to represent rough-water forms of more pyramidal habit and with more prominent outer cortical cell layers.

Some specimens of *Champia*, epiphytic on *Posidonia*, resemble *C. affinis* in that the segments are not distinct and a moderate number of outer cortical cells are present. The segments are, however, often distinctly longer than in the type of *C. affinis*, being 2-3(-4) times as long as broad. The longitudinal filaments often consist of 2-3 complete cells between the diaphragms, and the primary cortical cells are moderately conspicuous. Most of the plants with these characteristics are small and possibly young, though often fertile. For the present they are regarded as probably a form of *C. affinis*, but further studies on their seasonal growth and variation is needed. The specimens concerned include: Port Lincoln, S. Aust., 4-12 m deep, on *Posidonia* (Shepherd, 23.viii.1975; ADU, A46561, A46567, A46570), and Pig I, American R. inlet, Kangaroo I., S. Aust. (Womersley, 17.i.1947; ADU, A4467).

C. affinis differs from the other common southern Australian species, *C. zostericola*, in its habit, lack of hooked branches, and thick (2-3 layered) cortex which obscures both the diaphragms and the large primary cortical cells. The latter species is discussed further below, but very occasional plants with intermediate characters do occur. Harvey's Alg. Aust. Exsicc. 253H, distributed as *C. affinis*, is typical *C. zostericola*, and this has led to considerable confusion.

J. Agardh (1876, p. 304) distinguished two varieties of *C. affinis* (var. α *affinis* and var. β *intermedia*) on the proportions of the articulations and density of tetrasporangia. Both these features are unsatisfactory characters to separate varieties, and Kylin (1931, p. 28) considered var. *intermedia* as intermediate between *C. affinis* and *C. obsoleta*. These varieties do not appear worth distinguishing from the species.

Hooker & Harvey (1847, p. 402), following description of *C. affinis*, also described var. *arcuata*. This variety is considered specifically distinct and is relegated below to the synonymy of *C. zostericola* Harvey.

STRUCTURE AND REPRODUCTION

Material studied: Cape Lannes, S. Aust., low eulittoral (Reedman, 10.ii.1973; ADU, A42993 and 12.ii.1973; ADU, A42990); Nora Creina, S. Aust., lower eulittoral (Reedman, 12.ii.1973; ADU, A42994); and Pennington Bay, Kangaroo I., S. Aust., low eulittoral on reef (Reedman, 13.iv.1973; ADU, A42997).

Thallus development

There are 12-16 apical initials (Fig. 3B) which form a peripheral ring of longitudinal filaments; only very occasionally have filaments been seen within the periphery of the diaphragms. The initials segment (Fig. 3A) as do the peripheral apical initials in *C. viridis*, but the cortical layer of large cells cuts off small outer cells, at first around their outer margins, but a more or less continuous layer of small cells occurs on mature parts (Fig. 3G-I), and near the base (especially in older plants) a cortex several cells thick is developed (Fig. 3E). Hairs are commonly formed from outer cortical cells near branch apices. The diaphragms are formed usually by every third or fourth cell of the longitudinal filaments (Fig. 3A, D), leaving usually two or three complete cells between the diaphragms, each cell commonly bearing a gland cell. Rhizoidal development within the cortical layer has not been observed.

Branches arise from the region of the diaphragms, where a ring of outer cortical cells becomes meristematic and forms the apical initials of the branch. Branching occurs irregularly and often densely on all sides.

Procarp and carposporophyte

The supporting cell (Fig. 4A) is a large cortical cell in primary pit-connection with a longitudinal filament, and is generally attached opposite a gland cell. The cystocarps thus lie between the diaphragms of a branch, and cystocarpic plants are common. The supporting cell is multinucleate and densely cytoplasmic, and cuts off a 4-celled, curved, carposogonial branch (Fig. 4A), of which the first cell is binucleate and the other three uninucleate.

The supporting cell also produces a multinucleate, densely cytoplasmic auxiliary mother cell (Fig. 4A), which produces a uninucleate auxiliary cell just prior to fertilisation.

Following fertilisation, the pit-connections of the carposogonial branch cells enlarge (Fig. 4B) and the cells tend to fuse. Following presumed diploidisation of the auxiliary cell, first and then second gonimoblast cells are produced, and the latter divides further to produce a cluster of branched gonimoblast filaments (Fig. 4C, D), which terminate in uninucleate, ovoid carposporangia. The carposporangia mature simultaneously, but a new gonimolobe commonly develops from the basal cell of the gonimoblast and produces a secondary, later maturing, smaller cluster of carposporangia.

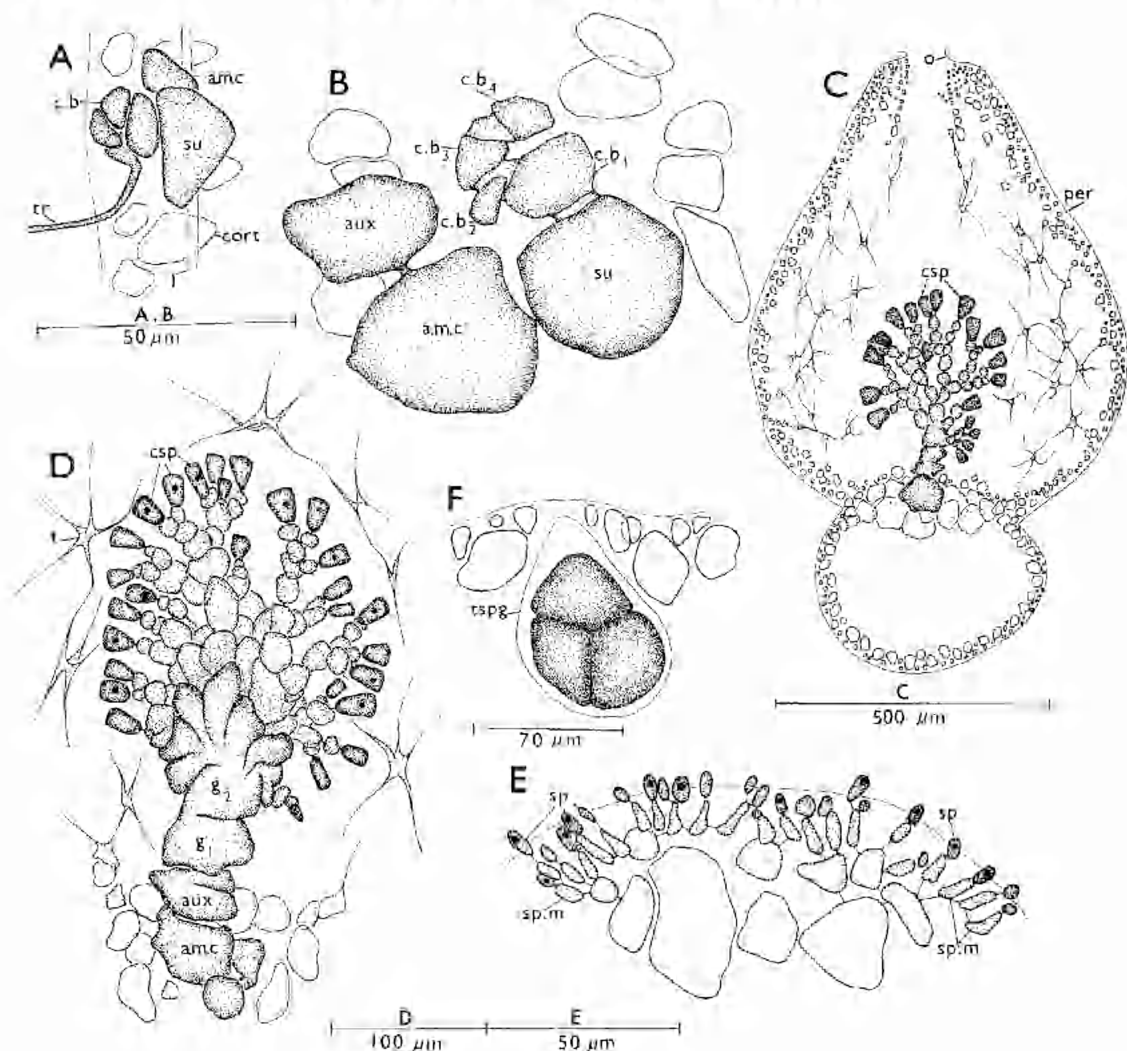


Fig. 4. *Champia affinis*. A. Supporting cell with auxiliary mother cell and carpogonial branch (A42990). B. Post-fertilisation stage with cells of carpogonial branch fusing (A42990). C. Section of an immature cystocarp showing development of carposporophyte from old auxiliary cell (A42997). D. A mature carposporophyte showing much-branched gonimoblast with terminal carposporangia, surrounded by cells of the "tela arachnoidea" (A42990). E. Section of male thallus showing development of spermatangia (A42997). F. Section with a mature tetrasporangium (A42993).

Vegetative cells adjacent to the auxiliary mother cell becomes densely cytoplasmic, and assist nutrition of the developing carposporophyte. Pit-connections between the lower cells of the gonimoblast enlarge considerably but the cells do not fuse completely.

As the gonimoblast develops, vegetative cells around its base divide to produce the pericarp. Inner cells of this form the cell reticulum, with an outer wall several cells thick (Fig. 4C). The mature cystocarp has a well-defined ostiole.

Spermatangia

Spermatangial mother cells are cut off from the small outer cortical cells to form a continuous layer over the branches, and each cuts off 2-3 ovoid spermatangia (Fig. 4E). Usually the entire spermatangium is shed.

Tetrasporangia

Tetrasporangia (Fig. 4F) develop by enlargement of inner cortical cells which develop several secondary pit-connections with adjacent cells. They are tetrahedrally divided,

with a thick gelatinous sheath, and usually densely scattered over the branches.

***Champia zostericola* (Harvey) comb. nov.**

Lomentaria zostericola Harvey 1855a: 545, 1863, synop.: 26, J. Agardh 1876: 632.

Gastroclonium (?) *zostericola* (Harvey) De Toni 1900b: 567.

Chylocladia zostericola (Harvey) Kylin 1931: 30.

Chylocladia affinis var. *arcuata* Hooker & Harvey 1847: 402. Womersley 1966: 150.

Lomentaria affinis sensu Kuetzing 1865: 31, pl. 86d-f. Sonder 1855: 523.

Champia affinis sensu King *et al.* 1971: 122. Lucas & Perrin 1947: 206, fig. 71, May 1965: 362. Shepherd & Womersley 1971: 165. Womersley 1950: 176.

Champia parvula sensu Harvey 1855a: 545 (in part).

FIGS 5, 6, 12C, 13

Thallus (Figs 12C, 13) usually spreading and forming irregular clumps with several branches from the entangled base, sometimes with one or more erect axes and spreading laterals, commonly 6 to 20 cm high, grey-red to red in colour, normally epiphytic on the seagrasses *Posidonia* and *Amphibolis* or on larger algae, possibly on rock; attachment at first by means of a small discoid holdfast with one to several axes, later attaching by small adventitious multicellular pads to the seagrass or itself. Axes usually 1½–3(–5) mm in diameter, branches only slightly slenderer and ultimate branches ½–2 mm in diameter, branches slightly basally constricted and with rounded apices; mature plants normally with some to many branches ending in recurved ("hooked") tips (Fig. 13); young branches distinctly constricted at diaphragms, segments mostly (½–) 1–1½ times as long as broad. *Diaphragms* distinct except in oldest parts of some plants, ½–1½(–2) mm apart. *Cortex* single layered, of relatively large angular cells [40–60(–75) µm across and mostly (1½–)2–4 times as long as broad] which are usually arranged more or less in longitudinal rows (Fig. 5E–H). Near the apices, each cell usually cuts off a single, relatively small cell from near a corner, and further such cells develop on older parts; however, the essentially single layered cortex of large cells is maintained throughout most of the plant (Fig. 5F, H). *Longitudinal filaments* confined to periphery of the diaphragms, rarely with odd ones more centrally placed, with generally one complete cell and two part cells between the diaphragms (Fig. 5C).

Cystocarpus subspherical to slightly conical, base broad and slightly constricted, 2–1 mm in diameter.

Spermatangia scattered over smaller branchlets, as extensive patches or collar-like sort around the diaphragms.

Tetrasporangia scattered over branches, 60–100 µm in diameter.

Type locality: Rottneest I., W. Aust.

Type: TCD (Harvey, Trav. Set 195).

Distribution. From the Abrolhos Islands, W. Aust. around southern Australia to Kiama, N.S.W. and around Tasmania. Generally epiphytic on seagrasses or other algae, from low tide level to 41 m deep, generally under slight to moderate water movement.

C. zostericola is based on small plants 3–4 cm high, growing on *Posidonia* (not *Zostera*). The type is No. 195 in Harvey's "Travelling Set", and his Alg. Aust. Exsicc. 294A (MEL 45197) from Fremantle (Fig. 12C) is very similar. Harvey was in the vicinity of Fremantle from April to June 1854, and during this period the plants are young (though often fertile), but may not show the typical hooked branches. Later in the year, especially in spring and early summer (September to November) the plants reach 20 cm in height and nearly all plants develop the hooked branches.

The lectotype (Fig. 13A) of var. *arcuata* Hooker & Harvey of *C. affinis* has been selected from several specimens in BM. It is a well-developed specimen, attached to stems of *Heterozostera* (?) and with numerous hooked branches. Whereas the type of *C. zostericola* is a young, small plant, that of var. *arcuata* is an older, larger plant of the same species.

The general confusion between *C. affinis* and *C. zostericola* (or *C. affinis* var. *arcuata*) is probably largely due to Harvey in his Alg. Aust. Exsicc. listing 253H from Western Port, Vic. as *C. affinis*, whereas these specimens are typical *C. zostericola*.

In contrast to *C. affinis* which is usually epiphytic on rough-water coasts and only occasionally occurs on robust algae or on seagrasses, *C. zostericola* is a common epiphyte on *Posidonia* and on some larger algae, usually in conditions of slight to moderate water movement and extending into deeper water.

The presence of hooked branches, the clearly septate thallus almost throughout, the essentially one cell thick cortex throughout the

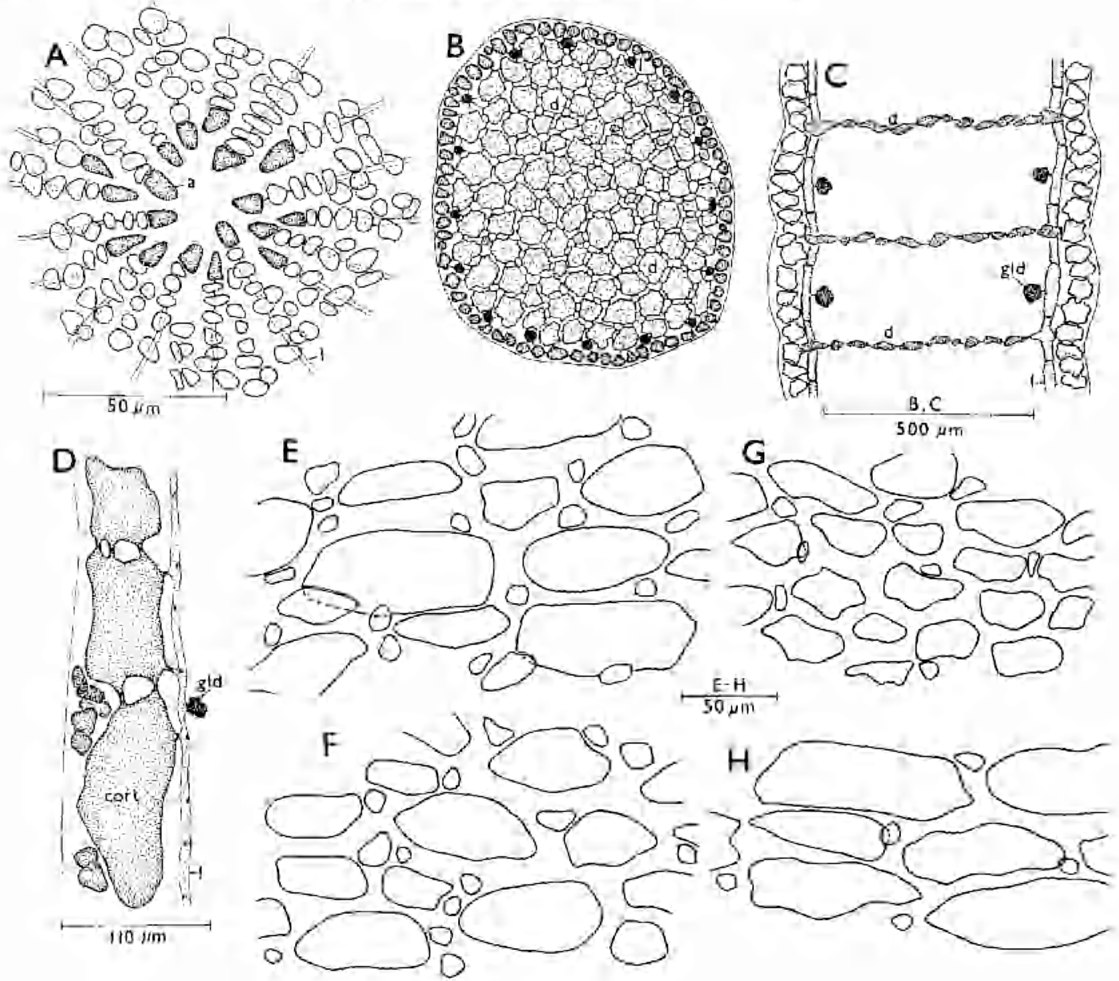


Fig. 5. *Champia zostericola*. A. Surface view of apex of branch showing apical cells (A43556). B. Cross section of branch showing cortex, diaphragm and peripheral longitudinal filaments (A43556). C. Longitudinal section of mature branch showing single layered cortex, diaphragms and longitudinal filaments with gland cells (A43556). D. Longitudinal section of an old axis showing slight development of small outer cells (A8944). E. Surface cell pattern of Harvey Alg. Aust. Exsicc. 249A (MFL. 45197), 10 cells from branch apex. F. Ditto, 30 cells from a branch apex. G. Surface cell pattern of the type specimen in BM of *C. affinis* var. *arcuata*, 10 cells from a branch apex. H. Ditto, 30 cells from a branch apex.

plant with few small cells lying largely between the primary ones, and the cortical cell dimensions and arrangement, characterise this species, but occasional plants occur without hooked branches. While most mature plants have several vague axes from their entangled bases, some (from Tasmania and Port Phillip Heads in particular) do have well developed main axes with abundant laterals. Such plants commonly (but not always) have hooked branches and have the single-layered, large-celled cortex typical of *C. zostericola*. However, the number of small cortical cells cut off

from the larger ones does vary somewhat, and very occasionally plants intermediate in this respect with *C. affinis* are found (see under *C. affinis*).

C. zostericola shows the variation in form which occurs in many other algal species distributed along all of southern Australia, i.e. the western specimens are generally smaller and less robust, and in the east, especially near Port Phillip Heads and in Tasmania, larger and more robust plants occur.

Variation in diameter of the branches and axes is considerable, probably largely depend-

ent on age, but branches are normally over 1 mm thick. However, new growth on older denuded branches may be slender and only about $\frac{1}{2}$ mm thick, as shown on several collections from Pearson I., S. Aust. in ADU.

Many references to *Champia affinis* apply, at least in part, to *C. zostericola* rather than to true *C. affinis* (see above). Probably most Australian records of *C. parvula* also apply to young plants of *C. zostericola*, though some may apply to slender *C. viridis*.

STRUCTURE AND REPRODUCTION

Material studied: Point Peron, W. Aust., drift (Gordon, 15.xi.1968; ADU, A34256); Port Noarlunga, S. Aust., 6-7 m deep on jetty piles (Johnson, 15.ii.1973; ADU, A43556); Marino, S. Aust., drift (Womersley, 26.x.1975; ADU, A46646).

Thallus development

There are 14-20 apical initials (Fig. 5A) which form a peripheral ring of longitudinal filaments (Fig. 5B), with only occasionally an odd inner one. The initials segment as in *C. affinis* and a single layer of large cortical cells is formed, arranged more or less in longitudinal lines (Fig. 5E-H). Fairly near the apices, these cortical cells become angular and cut off from a corner a smaller cell, which remains essentially in the layer of larger cells (Fig. 5E-H). The smaller cells are at first similar in number to the larger primary cortical cells, but later more may be formed; however, the cortex remains essentially only one cell thick throughout most of the thallus (Fig. 5C, D). The diaphragms are formed usually from alternate longitudinal filament cells, so that there is one complete longitudinal filament (with a gland cell) and two part ones between successive diaphragms (Fig. 5C). The relatively thin, essentially single layered cortex results in the primary cortical cells being visible throughout most of the plant, and the diaphragms are also conspicuous. Rhizoidal development within the cortex does not occur.

Branches arise from the region of the diaphragms, with their apical cells differentiating from the cortical cells. Near the base of entangled thalli, small branches may develop into haustorial pads of tissue and attach to other branches or to the host.

Many of the branch apices are curved or hooked (Figs 13B, 14A), and in some cases these aid in attachment. The only structural difference in hooked branch ends appears to be that on the convex side each segment has a greater number of cells than on the concave side.

Procarp and carposporophyte

From the limited female material available, the supporting cell of the procarp appears to be a large cortical cell, which produces the carpogonial and auxiliary cell branches (Fig. 6A). Following fertilisation, the pit-connections of the carpogonial branch cells enlarge (Fig. 6B) and the cells fuse, with a connection forming from the old carpogonium to the auxiliary cells (Fig. 6C).

The diploidised auxiliary cell cuts off a first gonimoblast cell which divides again (Fig. 6D) to initiate several branched gonimoblast filaments with the mature filaments terminating in single carposporangia (Fig. 6E) which mature simultaneously. New gonimolobes are produced from the base of the gonimoblast and mature later. Some darkly-staining and possibly nutritive cells occur around the base of the old auxiliary mother cell.

At an early stage in development of the procarp, cells are cut off from the surrounding cortical cells to form the protective pericarp (Fig. 6D). The inner cells of the pericarp form a reticulum (the "tela arachnoidea") which is gradually absorbed by the developing carposporophyte (Fig. 6E), and the outer 2-3 layers remain as the cystocarp wall, with a distinct apical ostiole.

Spermatangia

Spermatangia are formed as in other species, with small cells being cut off around the margins of the cortical cells and then producing branched chains of spermatangial mother cells over the surface, from which the elongate spermatangia develop.

Tetrasporangia

The tetrasporangia develop by enlargement of cortical cells (Fig. 6F) which protrude within the cortical layer, and they divide tetrahedrally (Fig. 6G).

Champia parvula (C. Agardh) Harvey 1853: 76. J. Agardh 1876: 303. De Toni 1900b: 558. Newton 1931: 439, fig. 263. Gayral 1966: 485, pl. 134.

Chondria parvula C. Agardh 1824: 207.

Chylocladia parvula (C. Agardh) Hooker. Harvey 1849: pl. 210.

Type locality. Gades (Cadiz), Spain.

Type. Herb. Agardh, LD, 26022.

Distribution. *C. parvula* appears to be the only species of *Champia* known from European coasts, and has been recorded from most temperate and tropical coasts of the world.

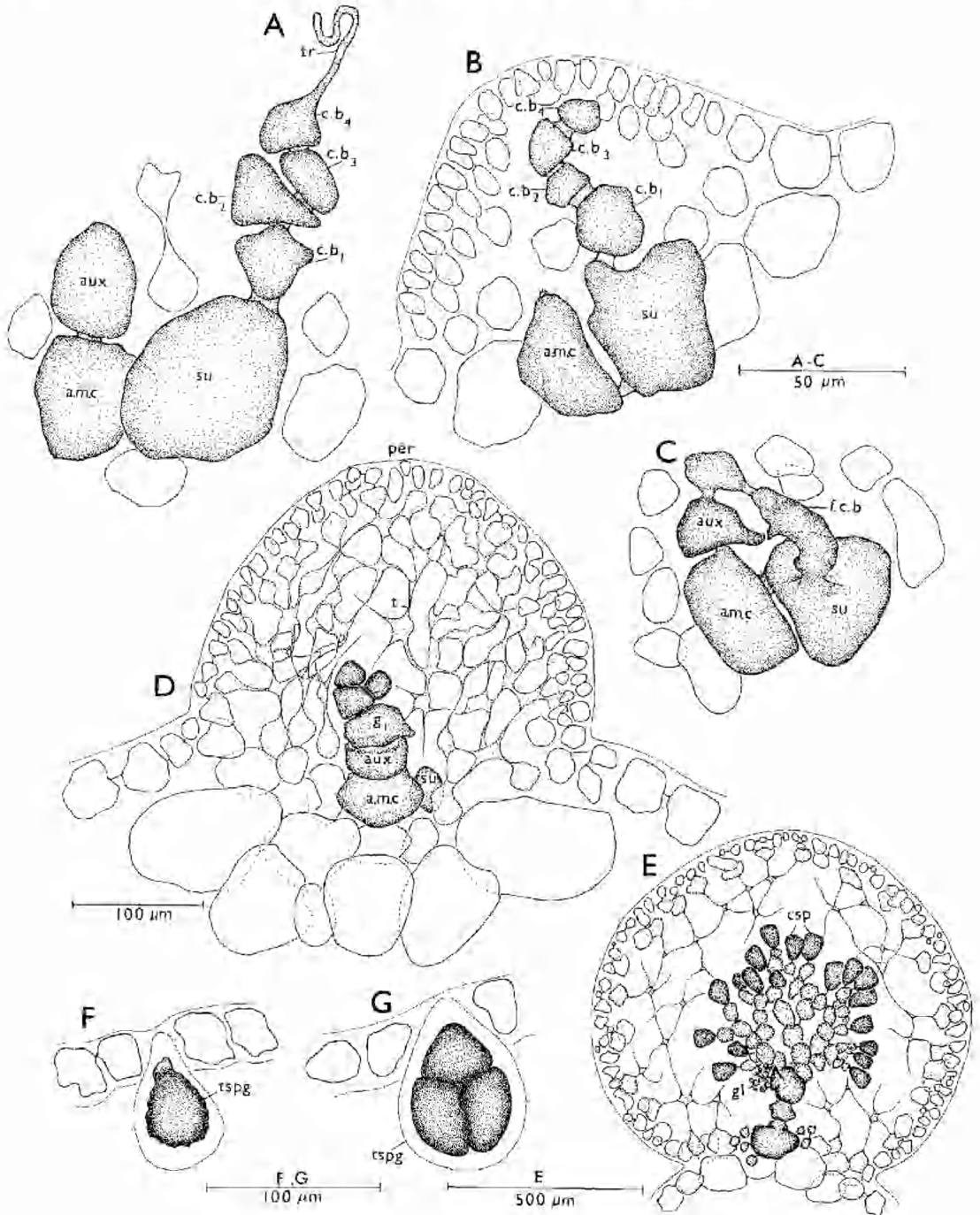


Fig. 6. *Champia zostericola*. A. Supporting cell with auxiliary cell branch and carpoogonial branch (A43556). B. An early post-fertilisation stage showing fusions between cells of carpoogonial branch (A43556). C. Post-fertilisation stage with fused carpoogonial branch and connections to auxiliary cell (A43556). D. Young gonimoblast within developing pericarp (A43556). E. Older carposporophyte with terminal carposporangia, within pericarp (ostiole not in section) (A43556). F. A young tetrasporangium (A34256). G. Mature tetrasporangium (A34256).

The following references credit *C. parvula* to southern Australia, but probably all apply to other species, mainly to small specimens of *C. zostericola*; in most cases it is not possible to clarify these references.

Guiler 1952: 94. Harvey 1855a: 545; 1859: 307. Lucas 1909: 34; 1929a: 19; 1929b: 50. Lucas & Perrin 1947: 206, fig. 70. May 1965: 362. Reinbold 1897: 53. Sonder 1846: 176; 1880: 17. Tate 1882: 18. Tisdall 1898: 506. Wilson 1892: 180.

C. parvula is generally recognised as a relatively small and variable species, and herbarium specimens credited to it vary in size, degree of branching, proportions of the segments and distinctness of the diaphragms, and in the size of the cortical cells and degree of outer cortical development. Harvey (1849, pl. 210; 1853, p. 76) commented on the variability of this species. In comparisons with southern Australian taxa, liquid preserved material from Ile Verte, Roscoff, France (*J. Feldmann*, 14.x.1974; ADU, A46057) has been taken as representing the species in western Europe. This specimen has longer segments (about as long as broad) than shown by Gayral (1966, pl. 134) but distinctly shorter than illustrated by Harvey (1849, pl. 210), and the diaphragms and cortical cells are distinct throughout the plant, with relatively slight development of small outer cells. There are usually two complete longitudinal filament cells between the diaphragms, and the longitudinal filaments are confined to the periphery of the diaphragms. The most detailed account of *C. parvula* is by Bliding (1928) who studied material from Woods Hole, U.S.A. Bliding's description and illustrations appear to agree with the Ile Verte specimen.

In spite of the several references to *C. parvula* in southern Australia, it now seems clear that typical forms of this species do not occur here. Young and small plants of *C. zostericola* do show some similarities, but are generally broader, more robust, and when mature have numerous hooked branches. Also, *C. zostericola* has usually only one complete longitudinal filament cell between the diaphragms, and the cortical cells are larger. Some small forms of *C. affinis* also approach *C. parvula* but can be distinguished on their greater outer cortical development. Harvey's specimens referred to *C. parvula* appear to be slender forms of either *C. zostericola* or *C. viridis*.

However, a distinctive taxon occurs epiphytic on *Amphibolis* at Tipara reef in Spencer Gulf, South Australia, and it appears best to

designate this as a distinct variety of *C. parvula*, to which it seems more closely allied than to the larger *C. zostericola*. Future studies may show that it should be recognised as a distinct species.

Champia parvula var. *amphibolis* var. nov.

FIGS 7, 14A

Thallus (Fig. 14A) erect, spreading, 3–11 cm high, with one to several much-branched main axes arising from a small discoid holdfast on stems of *Amphibolis*, red to red brown in colour, adhering to paper; occasional attachments by haustorial pads occur. *Axex* densely and irregularly radially branched to 3 or 4 orders, with alternate, opposite or occasionally whorled branches; axes 1–1½ mm in diameter below, tapering gradually to branchlets 1/3–½ mm in diameter. Young branches slightly constricted at diaphragms, segments 1–1½ times as long as broad, branch ends usually straight but rarely hooked, apices rounded. *Diaphragms* distinct throughout most of the thallus, somewhat obscured near bases of older plants. *Cortex* of a layer of angular cells 25–40(–50) µm across and (1–)2–3(–4) times as long as broad, with small cells cut off from their corners, and on older axes developing a continuous outer cortical layer (Fig. 7D) which in old plants may be 3 cells thick. *Longitudinal filaments* confined to periphery of diaphragms, developed from 10–15 apical cells, usually with two (–3) complete cells and two part cells between the diaphragms (Fig. 7C).

Cystocarps single, subspherical to urceolate, scattered over younger branches, 2–4½ mm long and 2–1 mm in diameter, ostiolate.

Spermatangia forming sori over several segments near the apices of young branches.

Tetrasporangia scattered in young branches, 75–120 µm in diameter.

Thallus erectus, effusus, 3–11 cm altus ex haptere parvo discoideo in Amphibole. Axes irregulariter ramosi, 1–1½ mm in diametro, ramuli 1/3–½ mm in diametro; segmenta 1–1½ plo longiora quam lata, Diaphragmata conspicua nisi prope bases plantarum veterum. Cortex compositus cellularum angulosarum 25–40(–50) µm latarum, (1–)2–3(–4) plo longiorum quam latarum, parvas cellulas in angulis ferens, ad 3 cellulas crassus in partibus veteribus crescens. Filamenta longitudinalia tantum in margine, 2(–3) cellulas totas inter diaphragmata habentia. Cystocarpia subglobosa vel urceolata, dispersa, 2–4½ mm longa et 2–1 mm in diametro, ostiolata. Spermatangia in soris fasciculata prope apices ramulorum. Tetrasporangia 75–120 µm in diametro dispersa.

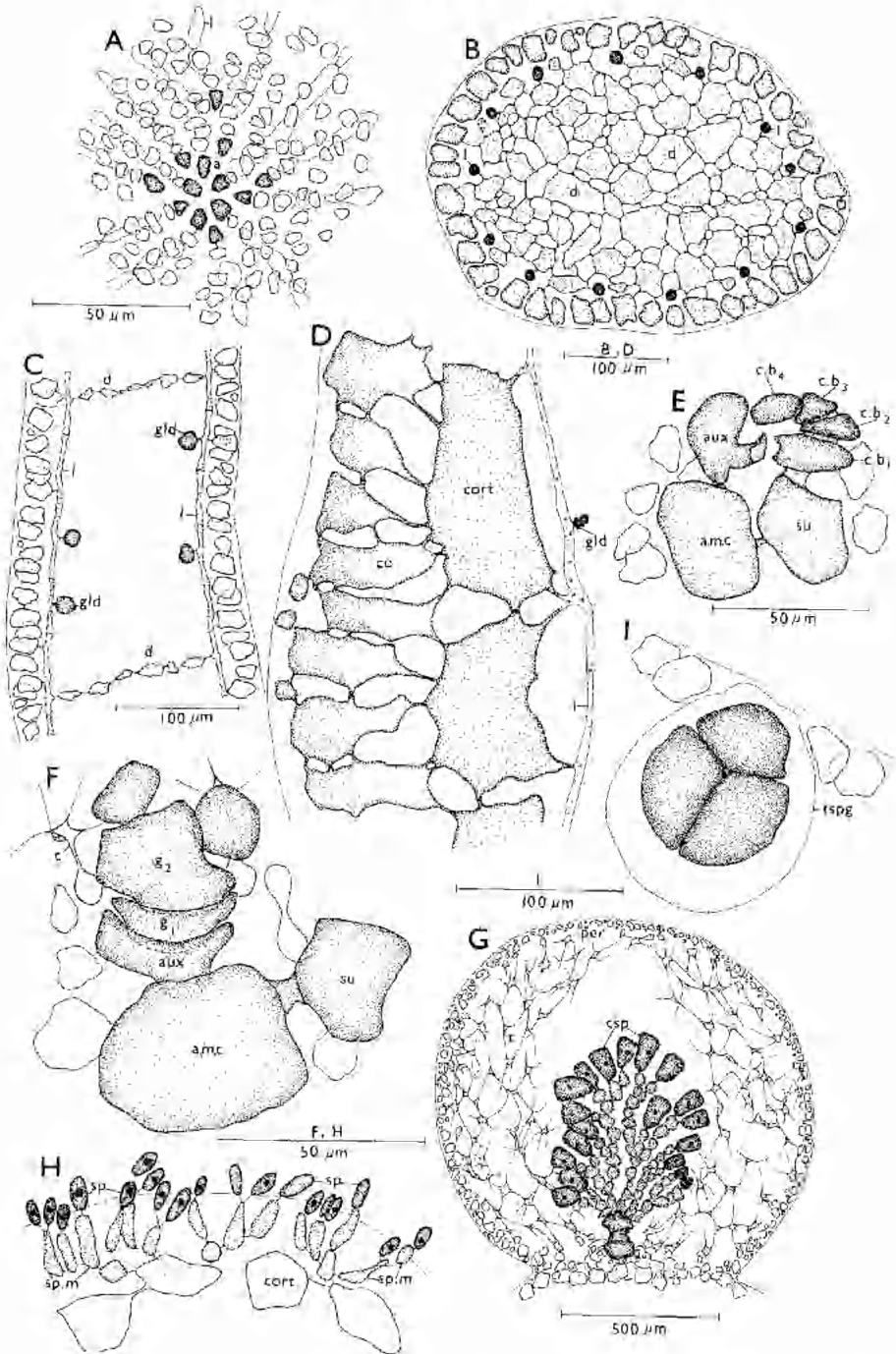


Fig. 7. *Champia parvula* var. *amphibolis*. A. Surface view of branch showing apical cells (A41276). B. Cross section of branch showing diaphragm, cortex and peripheral longitudinal filaments (A41276). C. Longitudinal section of a branch showing single-layered cortex, diaphragms, and longitudinal filaments with gland cells (A41276). D. Longitudinal section of older axis showing two (-3) layered cortex (A37291). E. Post-fertilisation stage showing fusions between carposporangial branch cells and connection to auxiliary cell (A38255). F. Young gonimoblast (A38255). G. Mature cystocarp (ostiole not in section) with carposporophyte bearing terminal carposporangia (A38255). H. Section of male thallus with spermatangia (A41276). I. Mature tetrasporangium (A37291).

Type locality. Tipara reef, Spencer Gulf, S. Aust. (*Shepherd*, 23.xii.1970).

Type. ADU, A38255.

Distribution. Known from several collections from Tipara reef, on *Amphibolis antarctica* and *A. griffithii*, 5–11 m deep. Young plants occur in June, maturing to bushy plants up to 11 cm high in December.

Var. *amphibolis* resembles the more typical forms of *Champia parvula* in being a relatively slender plant, mostly irregularly alternately branched, with diaphragms distinct throughout most of the plant and segments as long to slightly longer than broad, with the primary cortical layer of cells cutting off relatively few outer cells (except in old parts), and with usually two complete longitudinal filament cells between the diaphragms. Reproductively it is similar to the account of Bliding (1928) and at least superficially to the Ile Verte material.

It differs from European forms in being slenderer than some, more profusely branched, and in growing on *Amphibolis* as erect tufted plants. Future collections may show that it is not confined to this sea-grass and some specimens of Harvey (in TCD & MEL.) from Fremantle and King George Sound, W. Aust. (e.g. Alg. Aust. Exsicc. 254B in MEL, 45307) need careful comparison with this variety and with *C. zostericola*.

This Australian variety shows slight similarity to *C. zostericola* but is very much slenderer than most plants of the latter, only rarely has hooked branches, has longer segments close to the apices and has two complete longitudinal filament cells between the diaphragms rather than the usual one in *C. zostericola*. *C. zostericola* does occur on *Amphibolis*, but is more characteristically associated with *Posidonia*.

STRUCTURE AND REPRODUCTION

Material studied: Tipara reef, Spencer Gulf, S. Aust., on *Amphibolis*, *Shepherd*. The type, A41276 (13.xii.1971) and A37291 (30.ix.1970).

Thallus development

The thallus has 10–15 apical cells (Fig. 7A) which segment as in other species to form a peripheral ring of longitudinal filaments (Fig. 7B), with diaphragms forming usually from each third cell and thus with two (occasionally three) complete longitudinal filament cells (usually each with a gland cell) between successive diaphragms (Fig. 7C). The cortex is one cell thick (Fig. 7C) except on older axes

(Fig. 7D) and the elongate cortical cells cut off, from their corners, small cells (usually only one per cell) which lie more or less in the layer of primary cortical cells. These small cells commonly bear a hair in young branches, but such hairs are lost from older branches.

On old axes, the primary cortical cells cut off an outer, continuous, layer of cells (Fig. 7D) and this may become two or three cells thick, the outermost layer being of small cells.

Branching occurs from the regions of the diaphragms. Most branches are linear to the apex, but occasionally a curved or slightly "hooked" branch end occurs.

The holdfast remains small and discoid, but several new axes may develop from it. Small, pad-like haustoria also develop from branches of some plants, attaching mainly to other branches.

Procaryp and carposporophyte

The multinucleate supporting cell develops from a cortical cell and bears both carpogonial and auxiliary cell branches as in other species. Following fertilisation, the carpogonial branch cells begin to fuse (Fig. 7E) and a connection forms between the fertilised carpogonium and the auxiliary cell. The diploidised auxiliary cell forms a first gonimoblast cell which divides again (Fig. 7E), and the upper cell forms the branched gonimoblast filaments (Fig. 7G) which bear terminal carposporangia.

Following fertilisation, some vegetative cells around the supporting cell become darkly-staining, apparently as nutritive cells. Other vegetative cells divide to form the pericarp (Fig. 7G) which develops as in other species, with the inner cells forming the "tela arachnoidea" which is broken or absorbed by the developing carposporophyte. A well-defined ostiole occurs at maturity of the cystocarp.

Spermatangia

The small outer cortical cells, or further cells cut off from the primary cortical cells, divide to form branched filaments of cells covering the surface of one to several segments close to the apices of young branchlets. Each cell of these filaments functions as a spermatangial mother cell which cuts off outwardly 2–3 elongate-ovoid spermatangia (Fig. 7H), which appear to be shed entire.

Tetrasporangia

Tetrasporangia (Fig. 7I) develop within cortical cells which enlarge greatly and bulge within the segments of the thallus.

CHYLOCLADIA Greville

Chylocladia Greville (*in* Hooker 1833, p. 297), with the type species *C. kaliformis*, is conserved over *Kaliformis* Stackhouse 1809, and is distinguished from *Champia* by the formation of carposporangia directly from a large basal fusion cell (without branched gonimoblast filaments as in *Champia*) and by the cystocarps being non-ostiolate. Otherwise, *Chylocladia* is similar structurally to *Champia*.

While numerous Australian taxa have at some time been referred to *Chylocladia*, most have been placed in other genera (see Kylin 1931) or can now (see below) be excluded from *Chylocladia*.

However, a very distinctive species of *Chylocladia*, known from only a few deep-water collections, has recently been discovered in South Australian waters.

***Chylocladia grandis* sp. nov.**

FIGS 8, 9, 14B

Thallus: (Fig. 14B) erect, red-brown to red-purple, 20–50 cm high, with one to several axes arising from a hard, branched, perennial base to 5 cm high and 1/3–1/2 cm thick, attached to rock by a discoid holdfast to 1 1/2 cm across. Axes with opposite or usually whorled lateral branches to 10 cm long, similarly branched (mainly oppositely or alternately) to a second or third order; axes often denuded below, 2–7 mm in diameter, branches 1 1/2–2 1/2 mm in diameter tapering to 2–1 mm in diameter in branchlets; all branches slightly basally constricted, tapering gently to a rounded apex, segments 1/2–1 1/2 times as long as broad; branches slightly constricted between segments, but diaphragms conspicuous. *Cortex* in branchlets 1 cell thick (Fig. 8D), in older branches thicker and in axes to 8 cells thick (Fig. 8E); cortical cells ovoid, 25–35(–40) µm across and 1–2 times as long as broad in surface view. *Longitudinal filaments* scattered throughout diaphragms, with (1–)2(–3) complete cells and two part cells between the diaphragms (Fig. 8B), with each peripheral filament cell connected to the cortical cells by a lateral filament.

Cystocarps scattered over lesser branches, spherical to slightly ovoid, 1/2–1(–1 1/2) mm across, broad based, without an ostiole; carposporangia borne directly on the large, basal, fusion cell.

Spermatangia unknown.

Tetrasporangia scattered over branches, tetrahedrally divided, mostly 150–200(–250) µm in diameter.

Thallus erectus ad 20–50 cm altus, uno vel pluribus axibus ex base dura ramoso et perenni ad 5 cm altis et 1/3–1/2 cm latis ortis, haptere discoideo. Rami laterales in verticillum vel opposite dispositi, ad 10 cm longi et similiter ramosi; axes 2–7 mm, rami 1.5–2.5 mm et ramuli 0.7–1 mm in diametro, segmentis 1/2–1 1/2 plo longioribus quam latis, plus minus constrictis, diaphragmatibus conspicuis. Cortex ad unam cellulam in ramulis crassus, ad 8 cellulas crassus in axibus crescens. Filamenta longitudinalia dispersa, plerumque 2 cellulas totas inter diaphragmata habentia. Cystocarpia subglobosa 1/2–1(–1 1/2) mm lata, haud ostiolata, dispersa; carposporangia in coalescenti cellula ipsa magna basali portata. Tetrasporangia in ramis dispersa, 150–200(–250) µm in diametro.

Type locality. Tapley Shoal, Edithburg, S. Aust., 15 m deep (Shepherd, 2,ii,1969).

Holotype. ADU, A33515. Isotypes to be distributed under this number.

Distribution. Only known from the type collection from Tapley Shoal, and Investigator Strait, S. Aust., Watson, 11 m deep (20.i.1971; ADU, A40995), 23 m deep (28.i.1971; ADU, A41010), and 34 m deep (20.i.1971; ADU, A39197).

Chylocladia grandis appears to be quite distinct in its form, large size, dense branching, and in the perennial base which appears to last for several years, producing one to several fronds annually (probably in spring and lasting through summer).

STRUCTURE AND REPRODUCTION

Material studied: The type and Investigator Strait collections.

Thallus development

The multi-axial apex of a branch (Fig. 8A, B) includes both a central group of apical cells which give rise to the scattered longitudinal filaments, and outer apical cells which produce the peripheral longitudinal filaments and the cortex.

Fig. 8. *Chylocladia grandis*. A, Surface view of an apex showing peripheral and central apical cells (A33515). B, Longitudinal section of a branch apex showing development of cortex, diaphragms, and longitudinal filaments with gland cells (A33515). C, Cross section of a branch showing a diaphragm with sub-peripheral and central longitudinal filaments (A33515). D, Longitudinal view of outer part of a mature branch, showing the lateral connecting filaments between the longitudinal filaments and the cortex (A33515). E, Longitudinal section of an axis showing the multi-layered cortex (A33515).

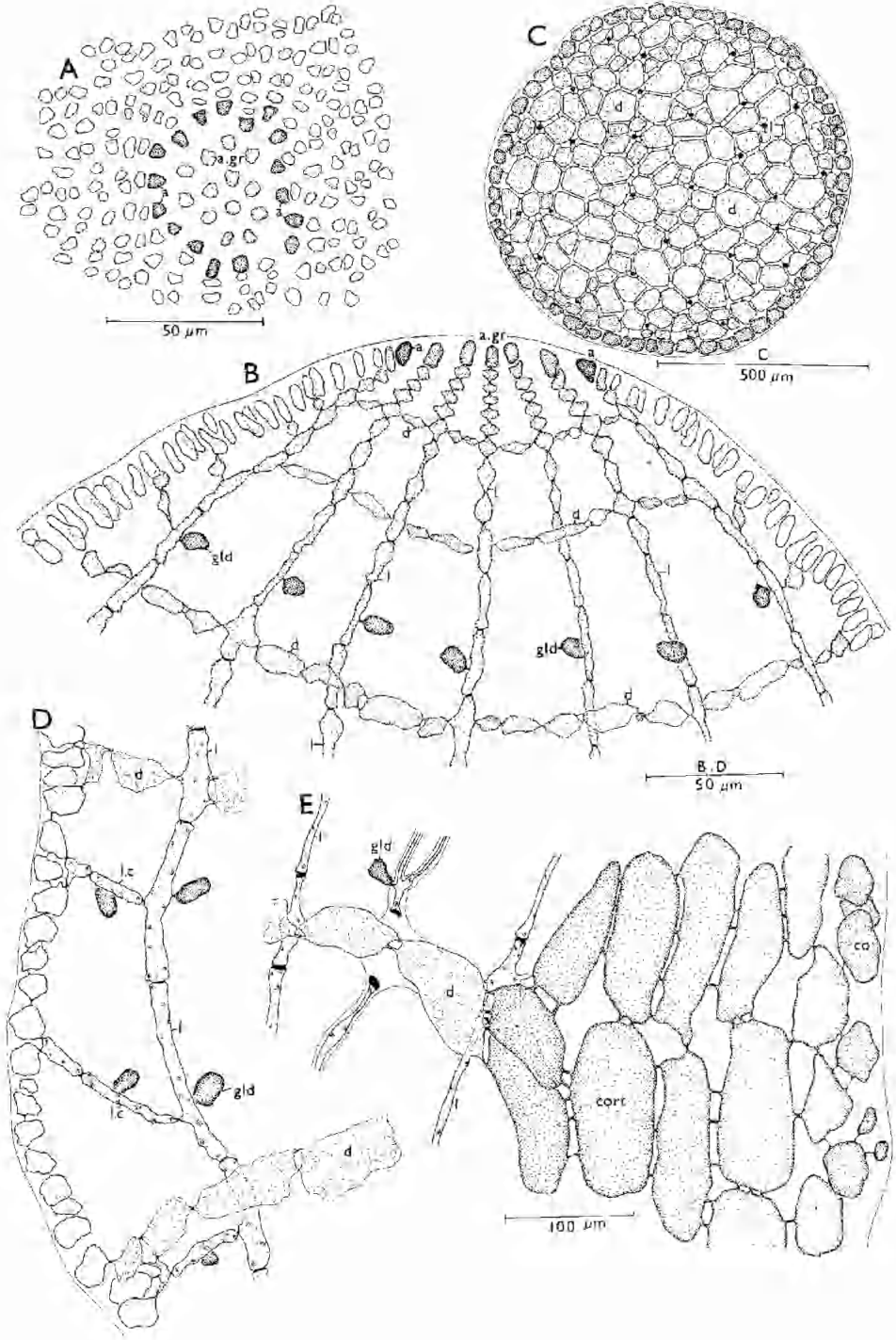


FIG. 8.

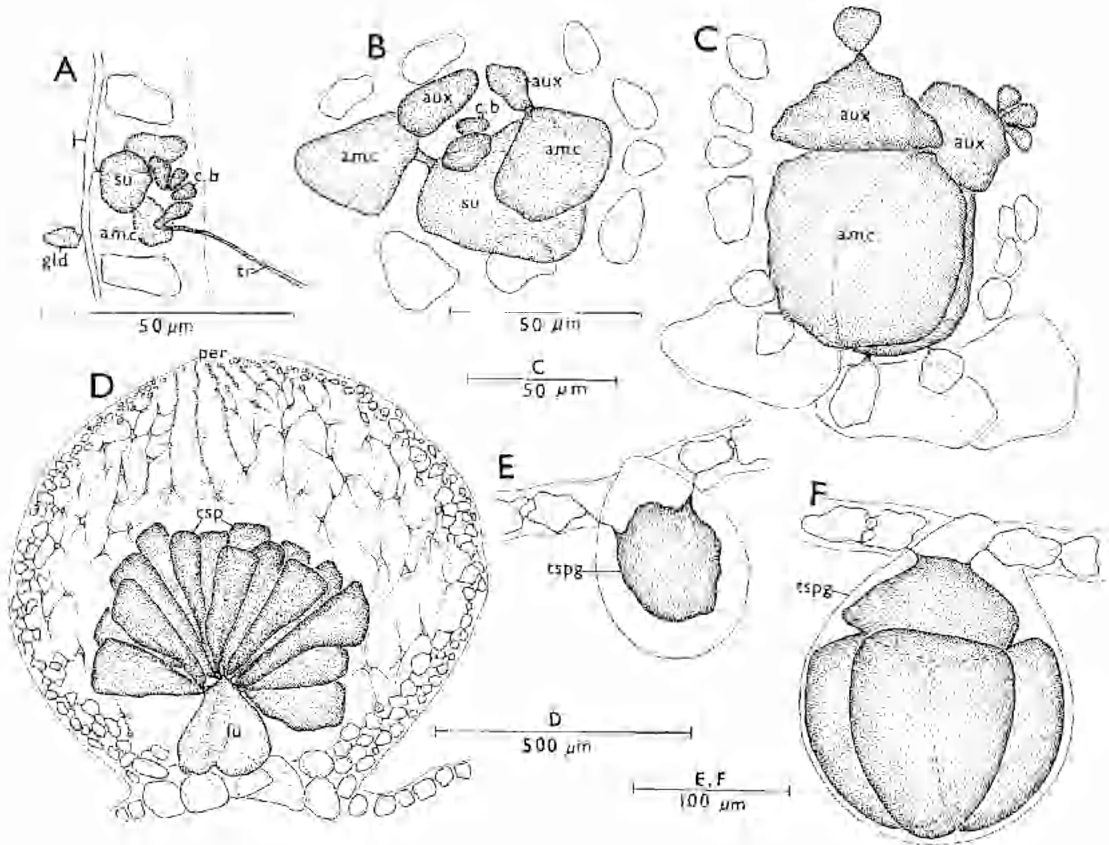


Fig. 9. *Chylocladia grandis*. A. Longitudinal section showing supporting cell with auxiliary mother cells and 4-celled carpogonial branch (A33515). B. Post-fertilisation stage showing two auxiliary cell branches and remnants of carpogonial branch (A33515). C. Post-fertilisation stage with auxiliary cells bearing young carposporangia. The supporting cell, auxiliary mother cells and auxiliary cells are partly fused (A33515). D. A cystocarp with mature carposporangia formed directly from the fusion cell, the lobes of which probably indicate the original auxiliary mother cells (A33515). E. A young tetrasporangium (A39197). F. A mature tetrasporangium (A39197).

The 12–16 central apical cells (Fig. 8A, B) divide transversely and the cells elongate to form longitudinal filaments. Each third cell usually produces a whorl of diaphragm initials which divide further to join with similar adjacent cells to form the single-layered diaphragms (Fig. 8B, C). The longitudinal filament cells between the diaphragms generally produce a single spherical to slightly pyriform gland cell (Fig. 8B).

The 15–20 outer apical cells divide transversely to form the peripheral ring of longitudinal filaments, but each of these cells, close to the branch apex, divides periclinally to form an outer primary cortical cell initial (Fig. 8B). This cell divides periclinally again once or twice and then the outer cell divides anticlinally to

form the primary cortical layer, but the later formed cells are not in pit-connection with the longitudinal filaments (Fig. 8B). The periclinial division of the cortical initial is followed by the inner one or two cells elongating to form a bridging filament between each cell of the peripheral longitudinal filaments and the cortical cells (Fig. 8D). This feature is not found in the Australian species of *Champia*. The peripheral longitudinal filament cells cut off diaphragm cells which join with those from the inner filaments. The peripheral filaments are usually separated by one diaphragm cell from the cortex (Fig. 8C).

Many of the primary cortical cells cut off a small outer cell which produces a hair; these hairs form a dense felt over most of the thallus.

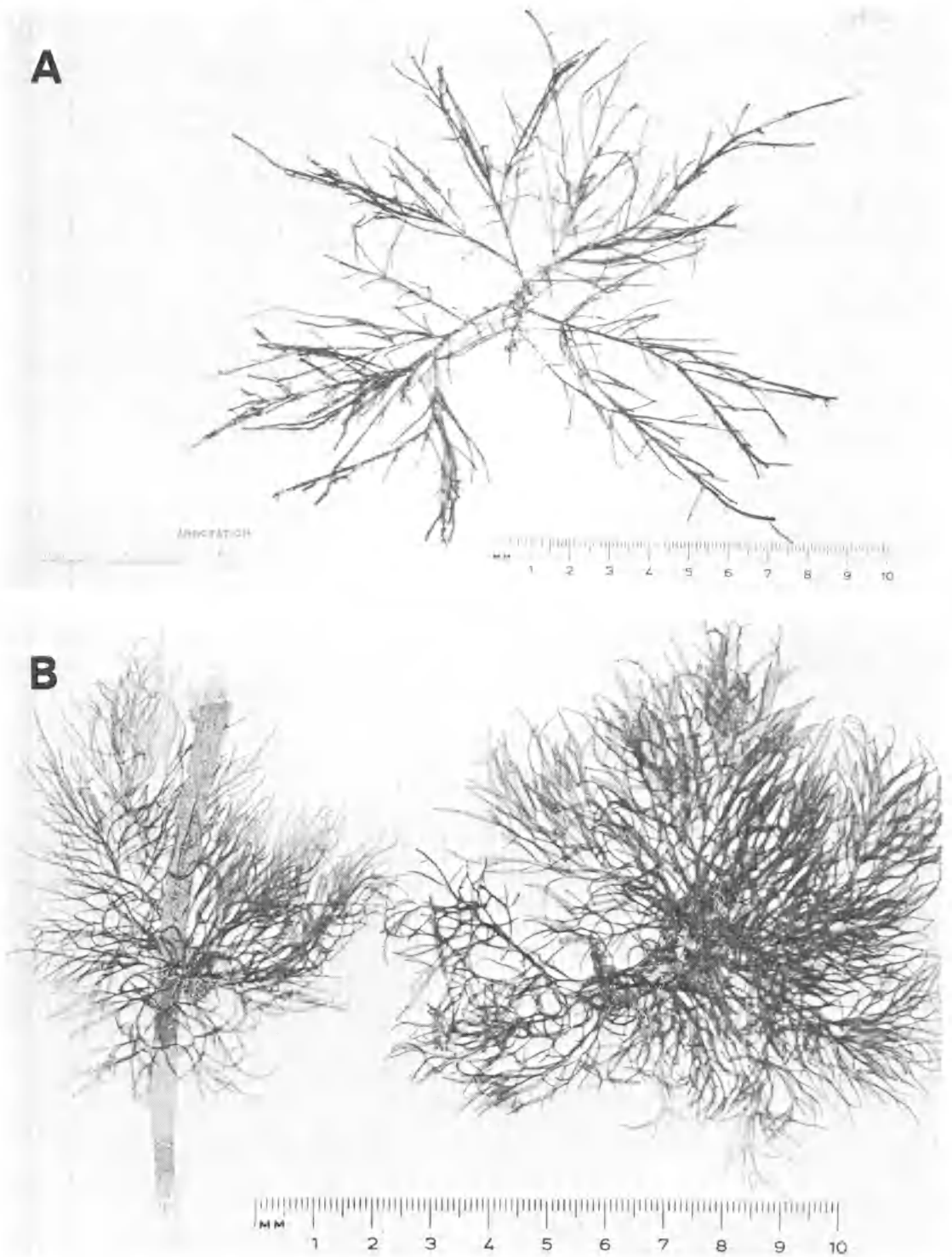


Fig. 10. *Champia viridis*. A. Type of *C. tasmanica* Harvey in TCD. B. A slender form (var. *gracilis* Harvey) on *Posidonia* (Marino, S. Aust. Drift. Womersley, 26.x.1975; ADU, A46651).

As the branch matures, the primary cortical cells cut off outer layers of cells, and in old axes the cortex may be up to 8 cells thick (Fig. 8E).

Branches originate from the region of the diaphragms, when a group of apical initials develops from the cortical cells.

The basal part of the thallus is clearly perennial, being hard and resistant, up to 5 cm high with irregularly placed, lateral projections representing the bases of previous axes. From the number and position of branch bases, some perennial bases appear to be 4–5 years old, and the axes are probably newly formed in spring and lost by the following winter. The branches probably decay rapidly since this plant has never been collected in the drift.

Procarp and carposporophyte

The supporting cell is a large primary cortical cell in pit-connection with a peripheral longitudinal filament (Fig. 9A). The supporting cell is multinucleate and cuts off outwardly a small cell, the carpogonial branch initial, and two larger cells, the auxiliary mother cells. The carpogonial branch (Fig. 9A) is 4-celled, curved, with an outwardly directed trichogyne. Prior to fertilisation, each auxiliary mother cell produces a uninucleate auxiliary cell (Fig. 9B).

Following fertilisation, a connection forms between the fertilised carpogonium and each auxiliary cell, and carposporangia are formed directly from the auxiliary cells (Fig. 9C). Fusion occurs between the auxiliary cells and auxiliary mother cells (Fig. 9D), forming a large basal fusion cell bearing the carposporangia directly. The supporting cell and some vegetative cells may be incorporated into the fusion cell.

Concurrent with the early development of the carposporophyte, vegetative cells around the supporting cell divide to produce erect chains of cells which cut off outer cells and form the pericarp (Fig. 9D), as in *Champia*. The inner cells of the pericarp form the "tela arachnoidea", but no ostiole is produced. When the carposporangia are mature, the top of the pericarp ruptures.

Tetrasporangia

The tetrasporangia develop by enlargement of the primary cortical cells (Fig. 9E), which have several pit-connections with adjacent cells. The tetrahedrally divided sporangia (Fig. 9F) develop a thick gelatinous sheath.

Relationships

Chylocladia grandis agrees well with *Chylocladia* and its type species, *C. kaliformis*, in thallus structure and in reproduction. However, it has not been established whether one or two auxiliary cell branches occur in *C. kaliformis*. *Champia* has only one auxiliary cell branch as far as is known, but the type of *Gastroclonium* Kuetzing (*G. ovale* (Hudson) Kuetzing) has two auxiliary cell branches (Bliding 1928, p. 27).

The thallus structure of *Chylocladia grandis* differs from that of the Australian species of *Champia* in that the initial cells of the primary cortex are connected to the longitudinal filament cells via a filament of one or two cells, not directly. Whether this occurs in *C. kaliformis* has not been established.

SPECIES EXCLUDED FROM CHYLOCLADIA

Apart from the various *Chylocladia* names which have been shown previously to be synonyms of species of *Champia* or other genera, the following names are now referred to other genera.

Chylocladia fruticulosa (Reinhold) De Toni 1900b: 576.

Lomentaria fruticulosa Reinhold 1899: 46.

Type locality. Investigator Strait, S. Aust. (Davey 148).

Type. Herb. Reinhold, M. Isotype in ADU, A1553.

The thallus of the isotype is on *Posidonia* (not *Amphibolis antarctica* as in Reinhold). It is hollow and without diaphragms, and the tetrasporangia are grouped in sori around depressions in the wall of the branches. These features are typical of *Lomentaria*, and the isotype (a small, bleached specimen) appears similar to the earlier described *Lomentaria australis* (Kuetzing) Levring 1946, p. 223 (*Chondrothamnion australe* Kuetzing 1865, p. 29, pl. 82 d–f). The southern Australian species of *Lomentaria* are in need of detailed study.

Chylocladia gelidioides Harvey 1863, synop.: 46. De Toni 1900b: 578; 1924: 312. Gepp & Gepp 1906: 257. Okamura 1904: 88.

Type locality. Twofold Bay, N.S.W. (*F.v. Mueller*).

Type. Herb. Harvey, TCD.

Although cystocarpic material has not been studied, the hollow thallus construction without single layered diaphragms, and sori of tetrasporangia, are typical of *Lomentaria*. The

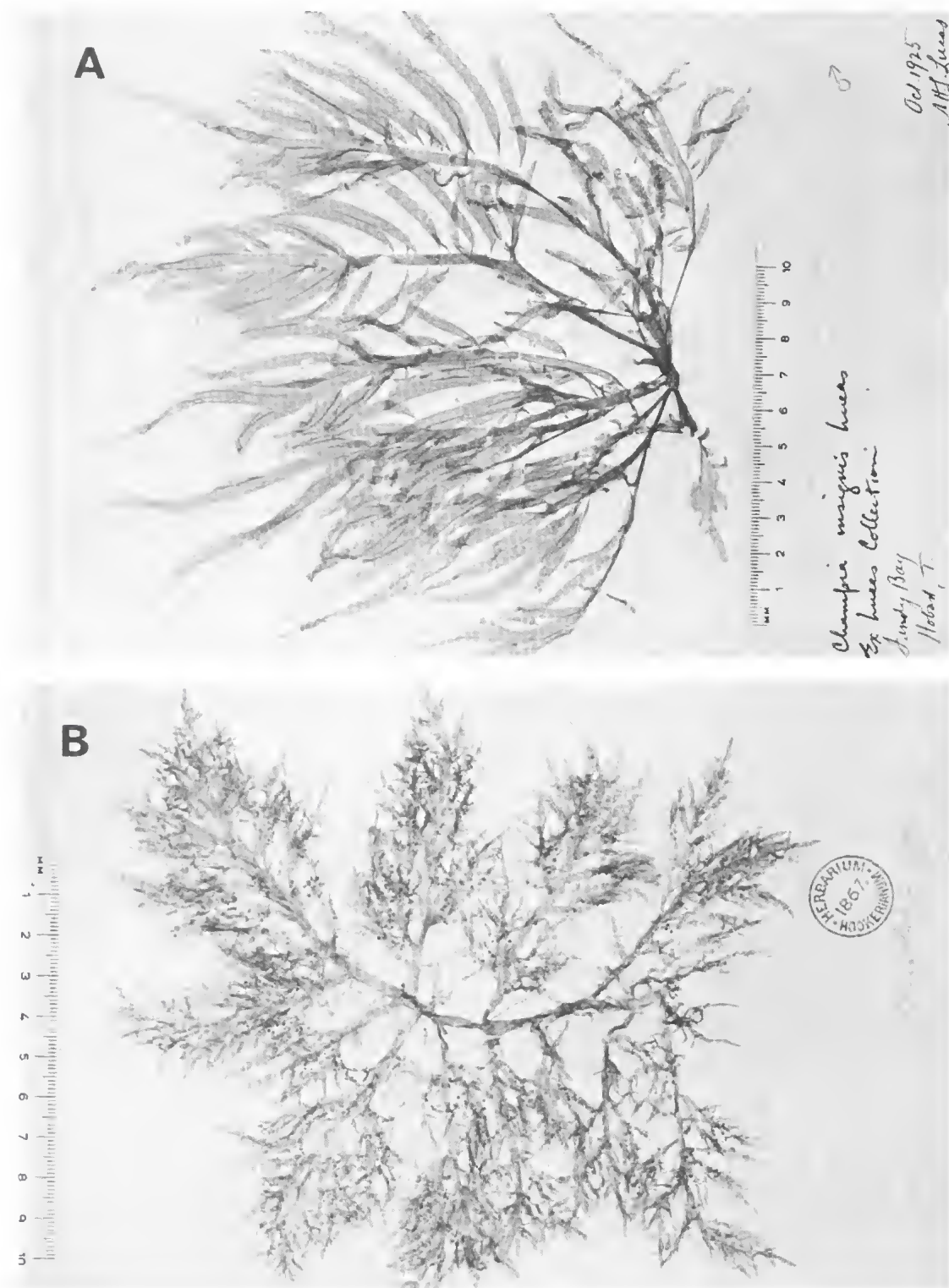


Fig. 11. A. *Champia insignis*. Isotype male specimen (ADU, A12237).
B. *Champia affinis*. Lectotype specimen in BM.

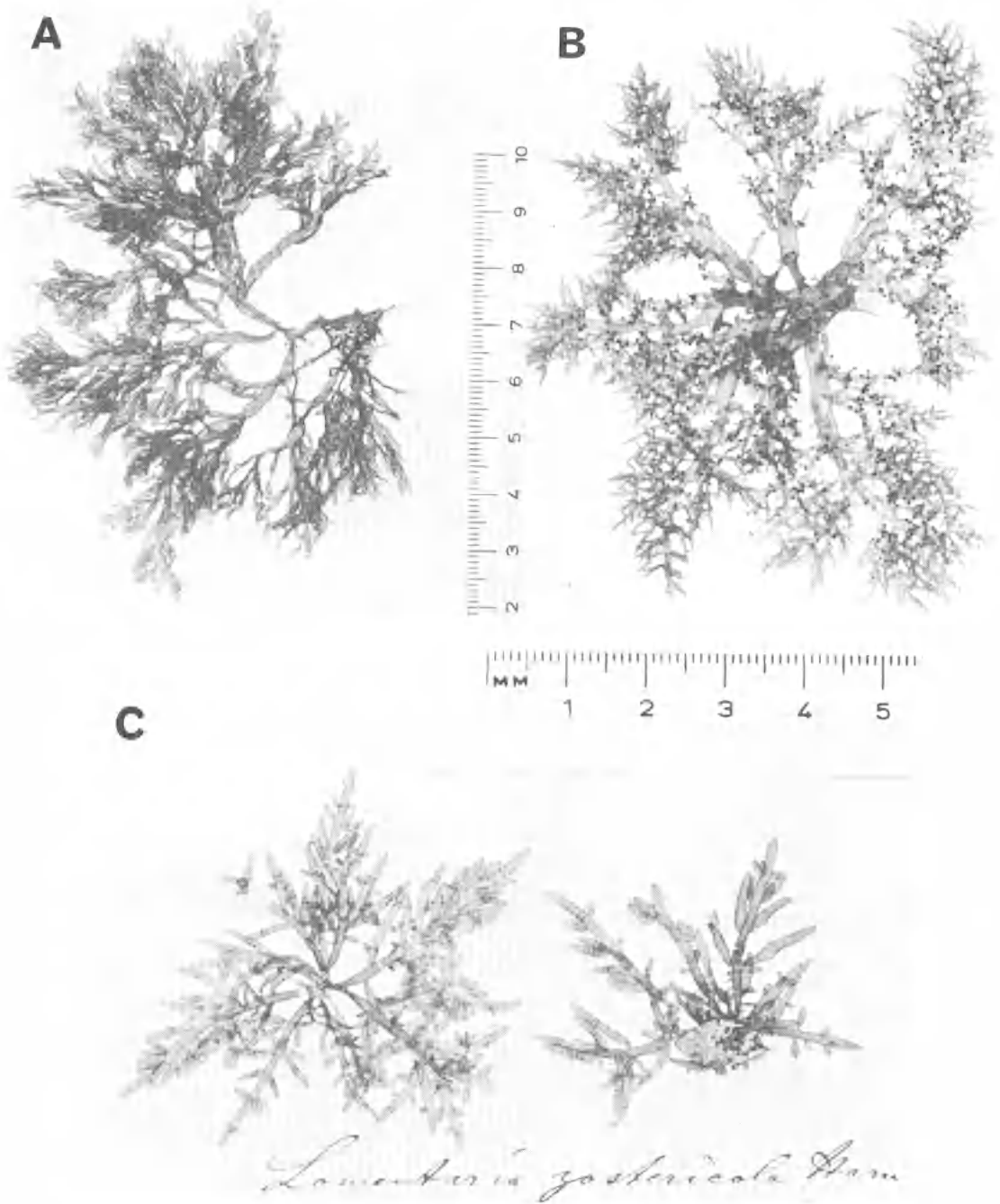


Fig. 12. *Champia affinis*. A. Harvey's Alg. Aust. Exsicc. 252I (as *C. obsoleta*) from Georgetown, Tas. (in TCD). B. Lectotype of *C. obsoleta* (Port Fairy, Vic. Harvey's, Alg. Aust. Exsicc. 252D) —a rough-water form. *Champia zostericola*. C. Harvey's Alg. Aust. Exsicc. 249A, Fremantle, W. Aust.

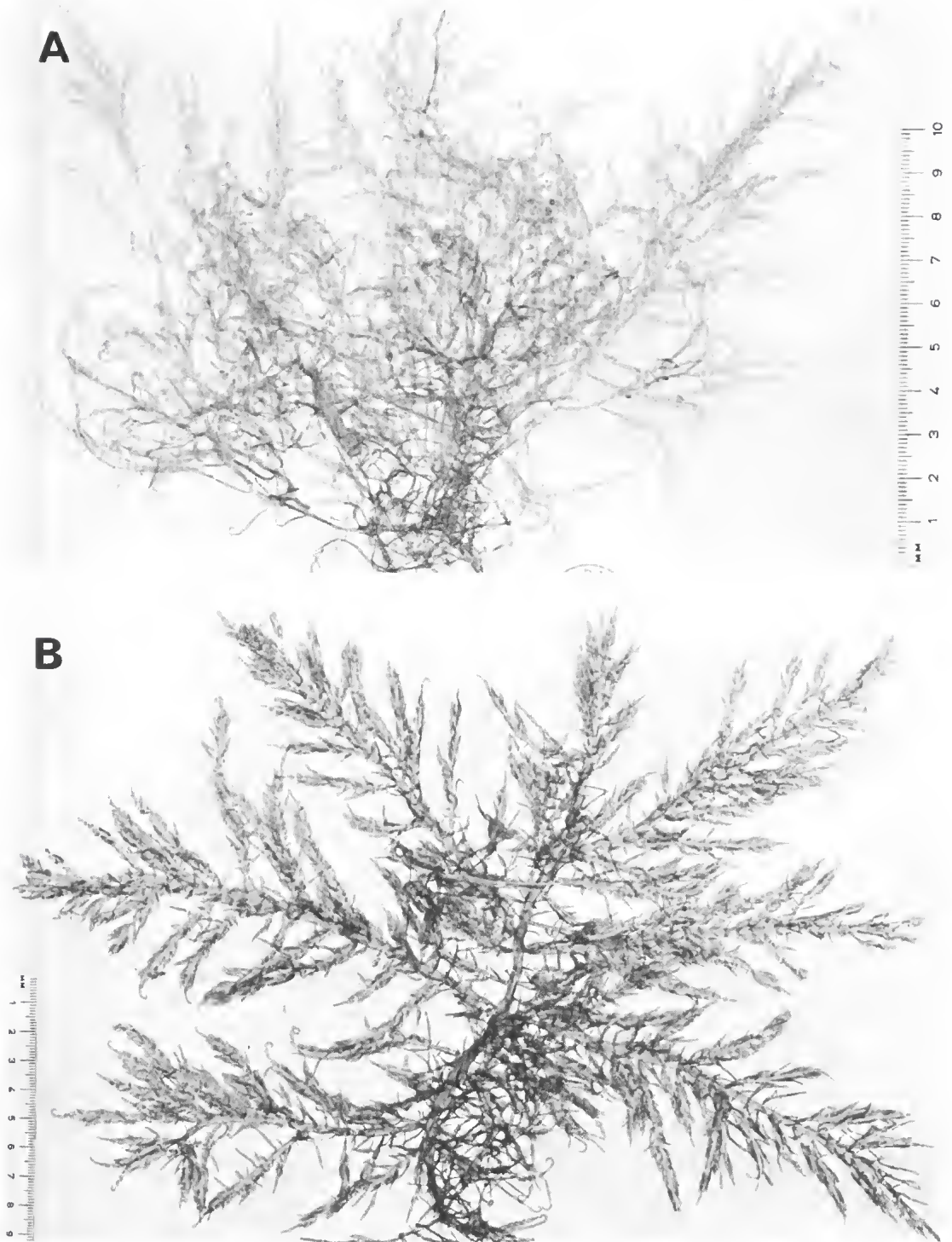


Fig. 13. A. Lectotype of *C. affinis* var. *arcuata* Hooker & Harvey. Gunn 1332, in BM. B. *Champia zostericola*, Musselroe Bay, Tas. Perrin, March 1937 (MEL 45252)—plant with well-developed axes.

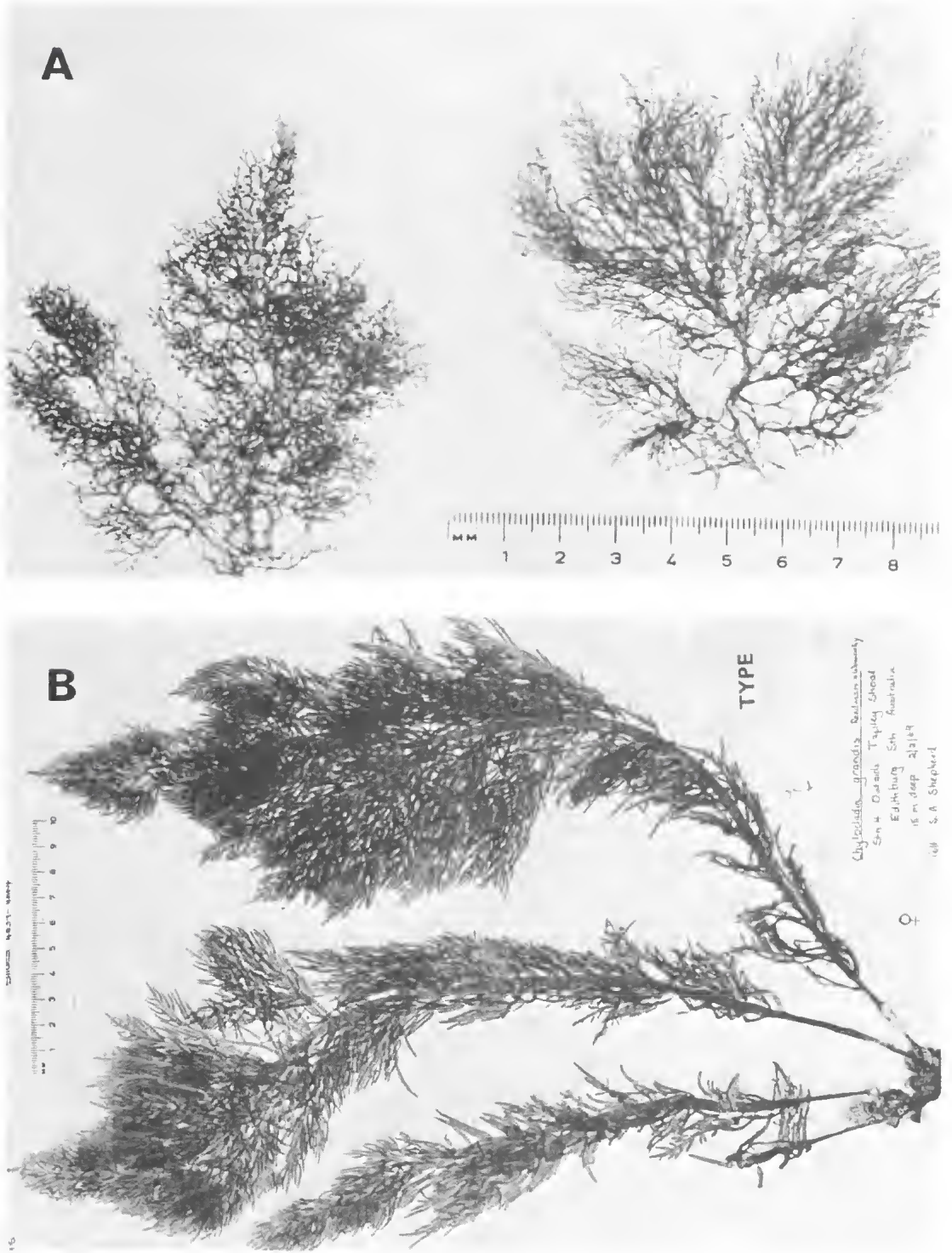


Fig. 14. A. *Champia parvula* var. *amphibolis*. Type specimen of variety.
 B. *Chylocladia grandis*. Holotype specimen.

thallus habit, cell detail, and tetrasporangial sori are very similar to *Lomentaria catenata* Harvey from Japan (as noted by Harvey 1863 and Okamura 1904), and the N.S.W. plant may be a slightly less robust form of the Japanese species, which is also recorded from Pacific Mexico by Dawson (1963, p. 465, pl. 92). It appears to be closely related to *Lomentaria ramsayana* (J. Agardh) Kylin (1931, p. 27, pl. 14, fig. 33).

Chylocladia multiramea Sonder 1853: 681.

Type locality, Lefevre Pcn., S. Aust.

Type, MEL, 45196.

The type specimen (female) in MEL is a slender, much branched, bleached plant of *Dasyphloea insignis* Montagne.

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